

## Relating fuel loads to overstorey structure and composition in a fire-excluded Sierra Nevada mixed conifer forest

Jamie M. Lydersen<sup>A,E</sup>, Brandon M. Collins<sup>A,B</sup>, Eric E. Knapp<sup>C</sup>, Gary B. Roller<sup>D</sup> and Scott Stephens<sup>D</sup>

<sup>A</sup>USDA Forest Service, Pacific Southwest Research Station, 1731 Research Park Dr., Davis, CA 95618, USA.

<sup>B</sup>Center for Fire Research and Outreach, College of Natural Resources, University of California, Berkeley, USA.

<sup>C</sup>USDA Forest Service, Pacific Southwest Research Station, 3644 Avtech Parkway, Redding, CA 96002, USA.

<sup>D</sup>Department of Environmental Science, Policy and Management, University of California, Berkeley, 130 Mulford Hall, MC#3114, Berkeley, CA 94720, USA.

<sup>E</sup>Corresponding author. Email: [jmlydersen@fs.fed.us](mailto:jmlydersen@fs.fed.us)

**Abstract.** Although knowledge of surface fuel loads is critical for evaluating potential fire behaviour and effects, their inherent variability makes these difficult to quantify. Several studies relate fuel loads to vegetation type, topography and spectral imaging, but little work has been done examining relationships between forest overstorey variables and surface fuel characteristics on a small scale (<0.05 ha). Within-stand differences in structure and composition would be expected to influence fuel bed characteristics, and thus affect fire behaviour and effects. We used intensive tree and fuel measurements in a fire-excluded Sierra Nevada mixed conifer forest to assess relationships and build predictive models for loads of duff, litter and four size classes of downed woody fuels to overstorey structure and composition. Overstorey variables explained a significant but somewhat small percentage of variation in fuel load, with marginal  $R^2$  values for predictive models ranging from 0.16 to 0.29. Canopy cover was a relatively important predictor for all fuel components, although relationships varied with tree species. White fir abundance had a positive relationship with total fine woody fuel load. Greater pine abundance was associated with lower load of fine woody fuels and greater load of litter. Duff load was positively associated with total basal area and negatively associated with oak abundance. Knowledge of relationships contributing to within-stand variation in fuel loads can increase our understanding of fuel accumulation and improve our ability to anticipate fine-scale variability in fire behaviour and effects in heterogeneous mixed species stands.

**Additional keywords:** fine fuels, forest structure, fuel model, overstorey composition, woody debris.

Received 19 April 2013, accepted 6 November 2014, published online 5 March 2015

### Introduction

Research and management in forests with altered fire regimes often focus on understanding and manipulating fuels. Surface fuels, consisting of flammable biomass within 2 m of the mineral soil surface (Keane *et al.* 2012a; Keane 2013), are of interest because these fuels drive fire behaviour and effects. Greater surface fuel loads increase potential surface fire flame lengths and can lead to canopy torching (Agee and Skinner 2005). In addition, high radiative and convective heat produced by intense surface fires is critical to the initiation and maintenance of crown fires (Wagner 1977; Scott and Reinhardt 2001). Surface fuels also influence fire effects on soils and understorey vegetation through their influence on fire severity and soil heating (Busse *et al.* 2005; Thaxton and Platt 2006; Rocca 2009; Webster and Halpern 2010). Smouldering combustion of duff may contribute to tree mortality, increase smoke production and influence

post-fire regeneration (Hille and Stephens 2005). In addition, knowledge of the rate of surface fuel accumulation is critical to understanding effectiveness and longevity of fuel reduction treatments (Stephens *et al.* 2012).

In mixed species forest types, small-scale (i.e. <0.05 ha) variation in species composition can have substantial effects on surface fuel properties, leading to differences in fire behaviour within a stand. Materials from different species may accumulate (Keane 2008a) or decompose (Stohlgren 1988) at varying rates. Needles of different species vary in burning characteristics such as maximum flame height and burn duration (Fonda *et al.* 1998; Fonda 2001). Needle morphology also leads to variation in fuel bed density, with long-needled pine species having fascicled needles accumulating a less dense litter layer that can contribute to greater fire intensity and spread (Weatherspoon and Skinner 1995; van Wagtenonk *et al.* 1998; Stephens *et al.* 2004; Knapp

and Keeley 2006). Locally dense accumulations of pine cones can also influence fire behaviour (Fonda and Varner 2004), and cones of different species and maturity levels can affect flame length and time (Gabrielson *et al.* 2012). In addition, fuel bed composition can influence the likelihood of secondary ignitions from firebrands (Ganteaume *et al.* 2009).

Although the importance of surface fuels is widely recognised, quantifying surface fuel loads can often be challenging due to their high spatial and temporal variability and multifarious nature (Arroyo *et al.* 2008; Keane *et al.* 2012b; Keane 2013). Field surveys are the most accurate method for estimating fuel loads, but they tend to be time consuming and expensive, making it difficult to cover a large area (Arroyo *et al.* 2008). Because of these limitations, it is often necessary to rely on surrogates for direct measurements of fuel loads, such as remote sensing or forest structure data. Remote sensing may be used to directly characterise fuels in forests but can be difficult because of the interference of vegetation canopies on measurements, particularly for fine fuels (Keane *et al.* 2001; Jakubowski *et al.* 2013). Studies have explored the relationship between forest overstorey and fuel bed characteristics, with a focus on general forest structural attributes such as basal area, cover type or stand age (e.g. Brown and Bevins 1986; Fernandes 2009; Parresol *et al.* 2012). Less information is available on within-stand variation in fuel loads and how this may correlate with tree overstorey structure and composition. These patterns can be hard to infer, as components of surface fuels vary at different scales (Fry and Stephens 2010; Keane *et al.* 2012b) and loads in different size classes are generally uncorrelated (Brown and See 1981; Brown and Bevins 1986; Keane *et al.* 2012a). Inaccurate inputs of fuel loading values due to lack of quantitative knowledge of spatial variability, coupled with the inability of many widely used fire behaviour models to incorporate finer scale variability in surface fuels, can lead to considerable errors in predictions of fire behaviour and spread (Keane *et al.* 2001; Bachmann and Allgower 2002). New methods are needed to provide better estimates of the variability in fuel loads on a smaller scale (Ottmar *et al.* 2012).

This study examines relationships between overstorey forest structure and composition and surface fuel loads in a Sierra Nevada mixed conifer forest that was logged in the 1920s and then recovered under fire exclusion. This management history is typical for many mixed conifer forests of California, as well as other forest types throughout the western US. Study objectives were to identify overstorey characteristics associated with loads of six surface and ground fuel components (1-, 10-, 100- and 1000-h woody fuels, litter and duff). We used mapped tree locations and intensive surface fuel inventories to analyse these potential associations at a small spatial scale (0.015 ha). Our intent was to help managers better understand how forest structure and composition influence variability in surface and ground fuels, because such relationships are poorly understood in Sierra Nevada mixed conifer forests. There are several possible applications of these potential relationships. Because overstorey measurements may be more readily available than fuels data, relationships between overstorey and fuels may allow for easier and more cost-effective fuel characterisations where specific fuel measurements are lacking (Keane *et al.* 2012b). A better anticipation of fine-scale variability in fuels could also

aid in prioritising areas for surface fuel reduction efforts based on improved understanding of overstorey characteristics that coincide with greater fuel loads or more reactive fuel complexes. Relationships could also aid in the development of thinning prescriptions that produce greater fuel discontinuity within stands, assuming that moderating surface fire behaviour and effects is a desired objective.

## Methods

### Study site

Sampling was done within 24 approximately 4-ha units established in mixed conifer forest as part of a larger study within the Stanislaus–Tuolumne Experimental Forest (Knapp *et al.* 2012). The study area is located on the western slope of the central Sierra Nevada in California at elevations ranging from 1585–1890 m. Annual precipitation averages 103 cm with the majority occurring from fall through spring and more than half falling as snow. Soils are deep and well-drained loam to gravelly loam derived from granite or tuff breccia (Wintoner–Inville families complex) (Knapp *et al.* 2013). Site productivity is high (Site Class I) (Dunning 1942). Dominant tree species are white fir (*Abies concolor* (Gordon and Glend.) Lindl. ex Hildebr.), sugar pine (*Pinus lambertiana* Douglas), incense cedar (*Calocedrus decurrens* Torr. Florin) and ponderosa pine (*P. ponderosa* Laws.). Jeffrey pine (*P. jeffreyi* Balf.) and black oak (*Quercus kelloggii* Newberry) are a less common component, and one live Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) tree was also present but its basal area was combined with that of white fir in the data due to the rarity of this species.

The last widespread fire at the Stanislaus–Tuolumne Experimental Forest occurred in 1889: prior to that the median fire return interval was 6 years (Knapp *et al.* 2013). Most of the merchantable timber was removed by logging operations in the late 1920s (Knapp *et al.* 2012). This history of fire exclusion and logging – two factors common to many mid-elevation forest stands in the Sierra Nevada – contributed to a shift in forest structure and composition, making the forest more susceptible to fires of uncharacteristic intensity and severity (Agee and Skinner 2005). Shrub cover at the site was low, averaging 2.5% (Knapp *et al.* 2013). Prior to data collection, no manipulation (except fire suppression) had taken place in any of the units since the 1928–29 logging.

### Data collection

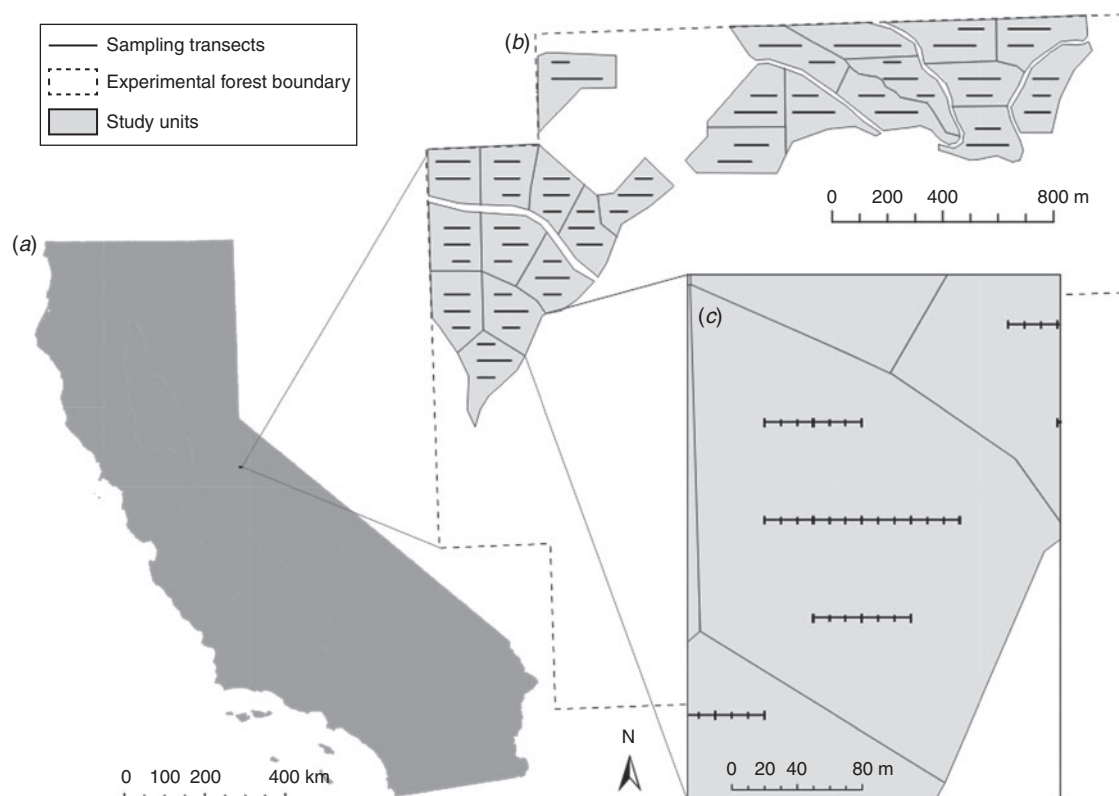
In each of the 24 units, a total of 240 m of fuel and canopy transects were established in an east–west direction. Transects were partitioned into 10-m sub-transects (Fig. 1). Nine measures of canopy cover were taken at 1-m intervals along each sub-transect with a sighting tube (densitometer), and covering species (or no cover) was recorded for each point. A greater number of readings may have given a more accurate measure of canopy cover, but the density of our sampling is similar to that used in other studies (e.g. Hall *et al.* 2006). Location (x- and y-coordinates relative to transect starting point), species and diameter at breast height (dbh) were measured for each tree and snag  $\geq 10$  cm dbh within 7.5 m of the fuels transect (belt transect of  $10 \times 15$  m for each sub-transect).

Surface fuels were measured using the planar intercept method (Brown 1974) along each 10-m sub-transect. Fuel components measured included duff, litter and four size classes of downed woody fuels: 1-h (0–0.6 cm diameter), 10-h (0.6–2.5 cm), 100-h (2.5–7.6 cm) and 1000-h (>7.6 cm). Intersects for the smaller woody fuel classes (1-, 10- and 100-h) were tallied by size class between metres 4 and 7 of the sub-transect (3-m sample length), and 1000-h fuels were measured by diameter along the entire 10-m distance. Litter and duff depths (cm) were sampled at points 2, 5 and 8 m from the beginning of the sub-transect. We did not measure the bulk density, but instead used equations quantifying relationships between depth and weight of litter and duff for common conifer species of the Sierra Nevada (van Wagtenonk *et al.* 1998). As our study site contains a mix of species, fuel loading constants were weighted by basal area of each species within each of the 24 units to account for differences in fuel characteristics across the study area (van Wagtenonk *et al.* 1996; van Wagtenonk *et al.* 1998). Although shrubs and herbaceous plants can contribute substantially to fuels in some forests, they were not included in this study due to their low abundance.

#### Statistical analyses

We used multiple linear regression with mixed models in SAS 9.3 (SAS Institute Inc. 2011) to examine relationships between overstorey variables and loads of duff and fine fuels (1-h, 10-h, sum of 1–100-h and litter). Due to the large number of

sub-transects with no 1000-h fuel loads, linear regressions were not done on this fuel class. We used the 10-m sub-transects as the measurement unit of interest because our intent was to look at small-scale variation of fuel loads and forest structure. Although we converted measures of forest structure and composition to average values within this  $10 \times 15$ -m area, presenting these measures at this scale provides some degree of spatial forest structure. To avoid the issue of pseudoreplication (Hurlbert 1984), sub-transects were not treated as independent replicates in analyses. Spatial autocorrelation of sub-transects was accounted for using a power spatial covariance structure based on the linear distance between sub-transects, and transect was included in the model as a random effect. Logarithmic and power transformations were applied to improve fit of the data to model assumptions of normality of residuals and equal variances. Transformations were chosen based on visual inspection of the distribution of residuals and the residual–quantile plots, with transformations chosen so that residuals were normally distributed (see Supplementary Material available online only). For each fuel component, we assessed models of all possible combinations of overstorey predictor variables up to a maximum of three variables per model. We compared the corrected Akaike information criterion (AICc) value for each model to assess the relative goodness of fit (Hurvich and Tsai 1989) and determine the best model for each fuel component. We also ran the model selection including all two-way interactions. All models including interactions were ranked very poorly by AICc



**Fig. 1.** Study site showing (a) location in California; (b) layout of study units (light grey polygons), with black lines showing location of all sample transects (240 m total in each unit) and (c) close up of one unit. Tick marks on transects delineate divisions between 10-m sub-transects (larger ticks are 30 m).

(AICc weight  $<0.02$ , see equation (1) below), so we did not include models with interactions in our assessment of relative variable importance (below). Because high levels of collinearity among predictor variables can complicate model interpretation (Freckleton 2011), we checked for collinearity among the predictor variables included in the best model for each fuel component. Correlations among covariates tended to be very low. Only three pairs of predictor variables had a coefficient of determination ( $R^2$ ) value  $>0.05$ : total canopy cover and total live basal area (BA) (0.15), white fir canopy cover and white fir live BA (0.19), and pine live BA and total live BA (0.38).

Using the best model (as determined by AICc) for each fuel component, we generated predictions and 95% confidence intervals of the mean fuel load when predictor variables are at their average value. We assessed the variance explained by fixed effects using the marginal  $R^2$  developed by Nakagawa and Schielzeth (2013). We examined the covariance parameters to assess the variance attributable to error and the random effects and covariance structure specified in the model. Wald tests were used to assess significance of covariance parameter estimates, and  $t$ -tests were used to assess significance of model coefficients and predicted values of fuel load. Estimates were considered significant for  $P$ -values  $<0.05$ .

We assessed the importance of predictor variables in two ways. First, we used AICc weights from all possible models to calculate an importance factor for each overstorey variable, representing its relative usefulness in predicting fuel loads (Burnham and Anderson 2002). AICc weights are calculated by normalising the likelihood of a given model  $m$  across all  $M$  models, and represent the relative likelihood of a model (Johnson and Omland 2004):

$$AICcWt(m) = \frac{\exp(-0.5 \Delta AICc_m)}{\sum_{i=m}^M \exp(-0.5 \Delta AICc_m)} \quad (1)$$

where  $\Delta AICc_m$  is equal to the difference in AICc values for model  $m$  and the minimum AICc value among  $M$  models. A higher AICc weight results when this difference is small. The importance factor (IF) for a variable  $X$  is then calculated by summing the AICc weights from all models in which that variable appears:

$$IF_X = \sum_{m \in M} AICcWt(m) \times I(X \in m) \quad (2)$$

where  $I(X \in m) = 1$  if  $X$  is contained in model  $m$  and 0 otherwise. Hence variables that appear in models with lower AICc values (and higher AICc weights) will have higher IF values. We also looked at the range of influence of the predictor variables included in the best model as assessed by AICc for each fuel component. This assessment of predictor variable importance is calculated by inserting the minimum and maximum value of a given covariate into the model regression equation, while holding each other covariate in the model at its mean value, to get a minimum and maximum predicted value of fuel load for that covariate. A greater range of influence indicates that a variable has an influence over a wider range of predicted values of a fuel component. This range of influence analysis was performed in R version 3.0.0 (R Core Team 2013).

We examined relationships between large woody fuels (1000-h) and overstorey variables with conditional inference tree analysis using the party package in R. This recursive partitioning method avoids the problem of overfitting without the need for tree pruning and prevents biased selection among covariates (Hothorn *et al.* 2006). We used a significance level of 0.05 for each split.

## Results

Overstorey structure was highly variable between sub-transects, as shown by the ranges and standard deviations of the overstorey variables (Table 1). For example, total live BA and stem density ranged from 0 to 271 and 0 to 2333, and standard deviations for individual species BA were close to or higher than the mean for all species. Excluding two sub-transects that had no live trees, the average percentage of shade-intolerant species (pine species and black oak) was 9.8% by stem density (trees  $>10$  cm dbh) and 16.7% by BA across all transects. The dominant species was white fir, comprising on average 51% of stems and 49% of BA within sub-transects. Dead BA (0–143.4) and snag density (0–933.0) were also particularly variable, with large standard deviations

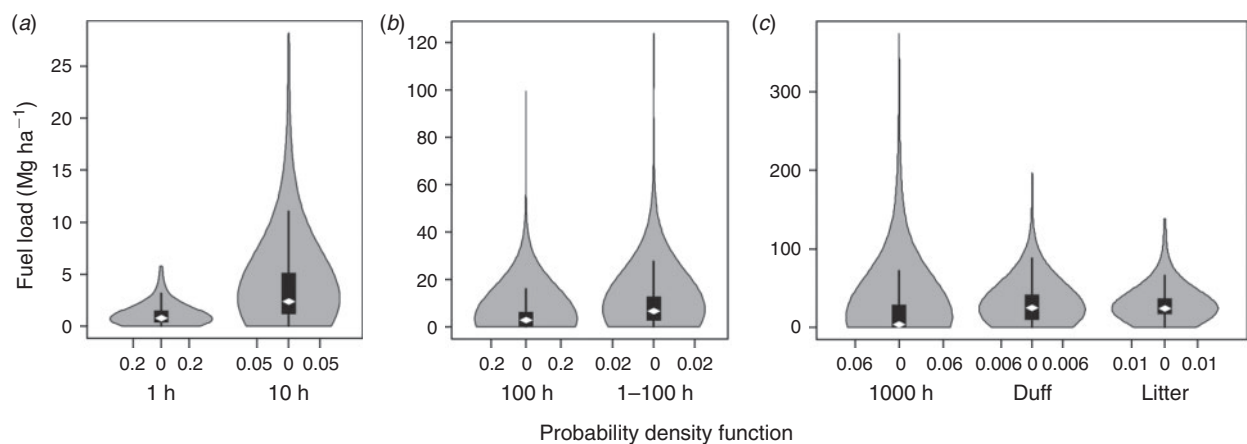
**Table 1. Observed values for fuel loads and overstorey variables**  
Averages and standard deviations were calculated using values from 10-m sub-transects ( $N = 576$ ); QMD is quadratic mean dbh of live stems

	Average	Standard deviation	Range
Fuel component (Mg ha <sup>-1</sup> )			
Duff	29.7	25.8	0–197.6
Litter	29.5	20.4	0–138.7
1-h	1.1	1	0–5.8
10-h	3.9	4.1	0–28.2
100-h	4.1	7	0–99.3
1–100-h	9.1	9.8	0–123.8
1000-h	23.7	43.3	0–374.3
Live basal area (m <sup>2</sup> ha <sup>-1</sup> )			
Total	67.5	39.4	0–271.4
Fir species <sup>A</sup>	33.8	30.2	0–186.5
Incense cedar	19.6	19	0–108.0
Pine species	14.0	24.7	0–140.3
Black oak	0.18	1.4	0–24.0
Dead basal area (m <sup>2</sup> ha <sup>-1</sup> )			
Total	12.2	17.6	0–143.4
White fir	8.9	15.7	0–143.4
Incense cedar	0.7	1.8	0–13.1
Pine species	2.5	8.1	0–128.2
Black oak	0.014	0.2	0–4.7
Stem density (ha <sup>-1</sup> )			
Live trees	713.9	344.7	0–2333.3
Snags	146.0	152.7	0–933.3
QMD (cm)	35.4	11.1	12.3–87.5 <sup>B</sup>
Canopy cover (%)			
Total	79.6	25.3	0–100.0
White fir	41.8	36.3	0–100.0
Incense cedar	21.1	28.5	0–100.0
Pine species	16.0	27.9	0–100.0
Black oak	0.68	7.0	0–88.9

<sup>A</sup>Includes data from one live Douglas-fir.

<sup>B</sup>Excludes data from two sub-transects that contained no live trees.





**Fig. 2.** Violin plots showing median (white diamond), interquartile range (black bar) and probability density (grey shaded area) of (a) 1- and 10-h, (b) 100- and 1–100-h, and (c) 1000-h, duff and litter. Note that the scales are different for the three figure sections. The grey shaded area is constructed from two vertically rotated kernel density plots. Data shown are for all sub-transects ( $N = 576$ ).

**Table 2.** Estimate and standard error for coefficients of overstorey variables included in the best model for each fuel component

Standard error shown is for the model coefficients; CI is the 95% confidence interval for the mean predicted fuel loads (lower–upper); predicted fuel loads are calculated at the average values of overstorey variables included in the model; BA is basal area; all coefficients and prediction estimates are statistically significant ( $P < 0.05$ )

	Coefficient	Standard error	Transformation	Prediction (Mg ha <sup>-1</sup> )	95% CI	R <sup>2</sup>
1–100-h						
Total dead BA (m <sup>2</sup> ha <sup>-1</sup> )	0.0050	0.0009	$y^{0.25}$	6.34	5.7–7.1	0.204
Fir live BA (m <sup>2</sup> ha <sup>-1</sup> )	0.0032	0.0006				
White fir canopy cover (%)	0.0028	0.0005				
Intercept	1.3000	0.0337				
1-h						
Total live BA (m <sup>2</sup> ha <sup>-1</sup> )	0.0087	0.0010	$\log(y + 0.1)$	0.74	0.7–0.8	0.273
Pine live BA (m <sup>2</sup> ha <sup>-1</sup> )	–0.0123	0.0016				
White fir canopy cover (%)	0.0052	0.0009				
Intercept	–0.8077	0.0758				
10-h						
Total live BA (m <sup>2</sup> ha <sup>-1</sup> )	0.0061	0.0009	$y^{0.4}$	2.87	2.5–3.3	0.251
Pine live BA (m <sup>2</sup> ha <sup>-1</sup> )	–0.0101	0.0013				
Total canopy cover (%)	0.0049	0.0011				
Intercept	0.8598	0.0935				
Duff						
Total canopy cover (%)	0.0363	0.0057	$y^{0.58}$	23.69	21.2–26.3	0.287
Total live BA (m <sup>2</sup> ha <sup>-1</sup> )	0.0305	0.0036				
Total dead BA (m <sup>2</sup> ha <sup>-1</sup> )	0.0238	0.0075				
Intercept	1.0358	0.4836				
Litter						
Total canopy cover (%)	0.0081	0.0016	$y^{0.4}$	25.72	23.8–27.8	0.159
Pine canopy cover (%)	0.0070	0.0015				
Total dead BA (m <sup>2</sup> ha <sup>-1</sup> )	0.0141	0.0023				
Intercept	2.7374	0.1432				

(Table 1). However, most (423 out of 576) sub-transects contained at least one snag. For snags, the average percentage of shade-intolerant species was 23.9% by stem density and 22.8% by BA.

Fuel load was similarly variable across the study site, with large ranges and high standard deviations for all fuel components (Table 1, Fig. 2). Fuel levels were mostly clustered towards the lower end of the distribution, with few plots having high values. Sub-transects with no 100-h or 1000-h fuels

recorded were common (46 and 47% of sub-transects), whereas duff and litter values tended to have somewhat less of a skewed or truncated distribution (Fig. 2). Duff and litter loads were high, with average depths of 1.9 and 3.1 cm.

Marginal  $R^2$  values for the predictive models were fairly low (0.235 on average), indicating that around one-quarter of variation in fuel loads could be attributed to overstorey structure at our study site (Table 2). Duff had the highest  $R^2$  value (0.287)

**Table 3. Covariance parameters for the best model for each fuel component**

The values shown for sub-transect are correlation coefficients reflecting spatial dependence of sub-transects. Values closer to 1 indicate spatial autocorrelation, whereas values closer to 0 would indicate no spatial relationship. Values for transect reflect the variance within transects, and values for residual show variation due to random error

Fuel component	Sub-transect	Transect	Residual
1–100-h	0.710	0.012	0.140
1-h	0.777	0.077	0.463
10-h	0.736	0.089	0.327
Duff	0.738	1.167	9.198
Litter	0.828	0.074	0.877

and litter had the lowest (0.159). We found a high spatial dependence of measurements based on covariance parameters for sub-transects, with values close to one indicating high correlation between nearby sub-transects (Table 3). Variance within transects was also significant for all fuel components, indicating that measurements were significantly correlated within transects.

High loads of fine woody fuels (1–100-h) were most strongly associated with total dead BA, live fir BA and white fir canopy cover (Tables 2 and 4). Live fir BA was the most important covariate, followed by canopy cover of white fir and snag BA (Table 4). Canopy cover of white fir influenced the predicted value of fine fuels over a relatively narrow range of values, whereas live BA of fir and total dead BA had an influence over a wider range of fine fuel levels (Fig. 3).

The highest 1-h fuel loads were associated with high white fir cover (Tables 2 and 4). The range of influence for white fir cover was small and focussed around the mean predicted fuel value, similar to the result for 1–100-h fuel load (Fig. 3). Live pine BA had a negative relationship with 1-h fuel load (Table 2) and also had a relatively small range of influence, mainly in the range of predicted values below the mean, whereas total live BA had a wider range of influence (Fig. 3). In addition to these three variables, live BA of fir had moderate influence (Table 4).

Ten-h fuel loads were associated with many of the same overstorey variables as 1-h fuels and the best predictive models for these two fuel components were very similar, with total and pine live BA and a measure of canopy cover included. For 10-h fuels, live pine BA again had a negative relationship with fuel load and influence in the lower range of fuel values, whereas total live BA had an effect over a wider range of values (Table 2, Fig. 3). One difference was that total canopy cover, rather than white fir cover, was associated with greater loads of 10-h fuel (Table 2). In addition, total snag BA was moderately important (Table 4).

Both duff and litter were positively related to total dead BA and total canopy cover (Table 2). In both cases, dead BA influenced the fuel level mainly above its mean predicted value, whereas total canopy cover had most of its influence below the mean predicted fuel load (Fig. 3). Greater litter load was also found in sub-transects with greater cover of pine (Table 2). In addition, live BA of pine species and canopy cover of white fir had some influence on litter loads (Table 4). Whereas for litter, total dead BA had the widest range of influence, for duff it did

**Table 4. Importance factors for all overstorey variables for each fuel component**

The shading corresponds to the importance factor value with darker highlighting for greater values. QMD is quadratic mean dbh (cm) of live stems

	1–100-h	1-h	10-h	Duff	Litter
<b>Live basal area</b>					
Total	0.070	0.854	0.989	1.000	0.055
Fir species <sup>A</sup>	0.924	0.146	0.011	0.002	0.001
Incense cedar	0.015	0.023	0.010	0.002	0.000
Pine species	0.050	0.854	0.989	0.002	0.135
Black oak	0.000	0.000	0.001	0.275	0.002
<b>Snag basal area</b>					
Total	0.826	0.000	0.171	0.306	0.999
White fir	0.049	0.000	0.009	0.045	0.001
Incense cedar	0.000	0.000	0.001	0.025	0.000
Pine species	0.000	0.000	0.001	0.031	0.000
Black oak	0.000	0.000	0.003	0.172	0.002
<b>Stem density</b>					
Live per ha	0.000	0.000	0.000	0.000	0.000
Snags per ha	0.091	0.000	0.068	0.001	0.000
QMD	0.001	0.000	0.000	0.007	0.060
<b>Canopy cover</b>					
Total	0.078	0.055	0.707	1.000	0.755
White fir	0.895	0.945	0.029	0.002	0.196
Incense cedar	0.000	0.076	0.000	0.029	0.007
Pine species	0.000	0.047	0.000	0.012	0.842
Black oak	0.000	0.000	0.000	0.011	0.000

<sup>A</sup>Includes data from one live Douglas-fir.

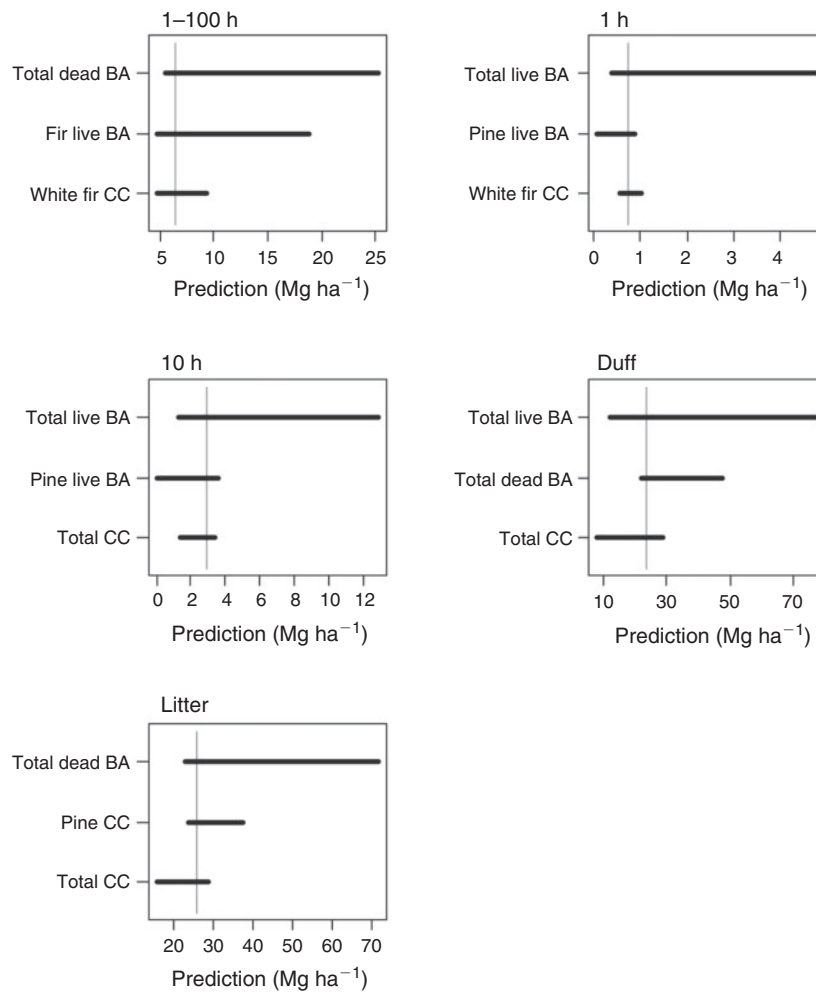
not influence the predicted value at the highest part of its range, and total live BA had the widest range of influence (Fig. 3). Duff load was also somewhat associated with live and dead BA of black oak (Table 4).

Greater 1000-h surface fuel loads were associated with greater total snag density (all species combined). The regression tree of 1000-h fuels had only one split ( $P < 0.001$ , data not shown), dividing sub-transects based on snag density. Among sub-transects with  $<333$  snags  $\text{ha}^{-1}$  ( $N = 527$ ), the level of 1000-h fuel load averaged  $21.1 \text{ Mg ha}^{-1}$ , whereas those with greater snag densities ( $N = 49$ ), averaged  $51.0 \text{ Mg ha}^{-1}$  of large fuels.

## Discussion

Establishing robust linkages between overstorey forest structure and surface fuel loads can be problematic because canopy and surface fuels can vary at different spatial scales (Keane *et al.* 2012a). In this study we demonstrate significant relationships between overstorey variables and surface and ground fuel loads, but only around 23% of the observed variation in fuel loads could be explained by the overstorey variables included in our analysis. Here we use these relationships to examine the relative influence of different overstorey variables on fuel loads, and discuss potential mechanisms. These relationships may enhance our understanding of fuel loads in forests with a history of logging and fire suppression.

Even though relationships between overstorey structure and fuel load components were statistically significant, each explained



**Fig. 3.** Range of influence of overstorey variables on fuel components, including all sub-transects ( $N = 576$ ). A greater range of influence indicates that a variable has an influence over a wider range of predicted values of a fuel component. Predicted fuel loads are shown for the best model (by AICc) for each fuel component. The vertical bar represents the mean predicted value of the fuel component. CC refers to canopy cover.

only approximately a quarter of the variation in fuel loads at our study site. The rest of the variation is presumably due to factors such as sampling error, weather (e.g. wind dispersion) and topographic influence on decomposition. Also, random effects of mortality and weather can substantially affect fuel patterns (Brown and See 1981). The low explanatory value of our models could also be due to a mismatch of sampling scale between overstorey and fuels (Keane *et al.* 2012b) and that a  $10 \times 15$ -m belt of mapped trees may be too narrow to adequately capture fuels dropped by tall trees. Overstorey structure and composition had the least influence on litter load ( $R^2$  of 0.16), indicating that these other factors may play a greater role in distribution of litter. This differs from the results of Hall *et al.* (2006), who found that among pools of downed fuels in ponderosa pine forests only litter was correlated with overstorey structure, with over 70% of the variability in litter pools being explained by canopy cover and BA.

Our field measurements were taken after many decades of fire exclusion. The average fuel loads in this study were similar to those typically reported for Sierra Nevada mixed conifer forests with a history of fire suppression (e.g. Stephens and Finney 2002; Innes *et al.* 2006). Different relationships and perhaps stronger correlations between overstorey and fuel loads may have been detected if sampling had occurred after a recent fire. Duff and litter loads in particular are typically strongly associated with time since past fire (Parresol *et al.* 2012), and burn conditions can additionally influence the pattern of fuel consumption in relation to the overstorey (Hille and Stephens 2005). In the absence of fire, fuels in Sierra Nevada mixed conifer forests reach a saturation point where accumulation rates equal decay rates after about 30 years (Kittredge 1955; van Wagtendonk and Sydoriak 1987; Keifer *et al.* 2006), although accumulation of large woody debris may continue after other fuel classes have reached equilibrium (Stohlgren 1988).

However, fuel decomposition rates may depend on temperature and relative humidity (Keane 2008b), which are also influenced by overstorey structure. Therefore, within-stand variation in fuel load could occur due to microclimate effects as well as species-specific inputs in forests with a long fire-free interval such as our study site.

The skewed distribution of fuels found in this study, indicative of a heterogeneous rather than uniform fuel bed, is typical of forest fuels (e.g. Brown and See 1981; Brown and Bevins 1986; Keane *et al.* 2012a). Fuels in the 100- and 1000-h classes had particularly skewed distributions, evident by the long and thin tail of the distribution relative to the interquartile range (Fig. 2), suggesting patchy loads across the study area. Perhaps longer sampling transects would have allowed for greater detection of large woody fuels and thus better relationships with overstorey variables. Our findings are similar to those of Fry and Stephens (2010) for an old-growth Jeffrey pine mixed conifer forest. They demonstrated that large fuels were infrequent, but tended to occur with high loads when present (up to 210 Mg ha<sup>-1</sup>); that is, highly clumped spatially. In our study, the finding that higher 1000-h fuel loads corresponded to greater total snag density suggests that tree mortality, which is often spatially clumped (Lundquist 2007), is a possible mechanism driving the patchy occurrence of pockets of high coarse fuel loads. Greater mortality can occur in areas of high tree density, and is generally due to a combination of factors including diseases, insects and environmental stressors (Smith *et al.* 2005).

Fine fuels tended to have a comparatively less skewed distribution across our study area (Fig. 2). This is likely due to the inputs for fine fuels (small branch wood) being more constant than that of coarse fuel (large branches, tree boles) (Keane 2008b) and greater dispersion when falling through the air than with the larger and heavier fuels. Additionally, as Keane *et al.* (2012b) demonstrated, surface fuels in smaller size classes tend to be more strongly correlated at smaller spatial scales compared with larger fuels; thus it would be more likely to find a uniform distribution at the scale of our sampling (0.015 ha).

This study found that measures of total BA and canopy cover were relatively important covariates for predicting fuel loads, with the best model for each fuel component containing either total live or dead BA or total canopy cover, but including variables pertaining to individual species improved model fit for all surface fuel components. Associations between within-stand species composition and fuel load characteristics have been previously found in both a dry mixed conifer forest (Fry and Stephens 2010) and a eucalyptus woodland (Duff *et al.* 2013). In addition, differences in deposition rates for different species and size classes of Sierra Nevada trees have been demonstrated (van Wagtenonk and Moore 2010). This suggests that although the influence of overstorey composition may be modest, as at our study site, within-stand species composition is worthy of consideration.

In this study, live and dead stem density were not important predictive factors for any fuel component. Instead, measures of total or individual species BA often had high importance factors. BA is a better indicator of aboveground biomass and, therefore, potential fuel load. As BA tends to be more reflective of the presence of large rather than small trees, this finding suggests that large trees have a disproportionate influence on surface fuel

accumulation (Collins and Stephens 2007; van Wagtenonk and Moore 2010). BA of individual species was also assessed, and BA of pine or oak was among the important predictive factors for several fuel components (e.g. 1-h, 10-h, litter and duff). This suggests that even the less abundant species may play a role in predicting fuel loads (Fry and Stephens 2010).

The negative relationship between 1-h fuel loads and pine BA found in this study (Table 2) is consistent with findings of others evaluating the effect of cover type (Brown and Bevins 1986), within-stand species dominance (Fry and Stephens 2010) and species-specific inputs (van Wagtenonk and Moore 2010) on fuel bed characteristics. Pines drop fewer woody fuels in the smallest size class, as they may lack branches of sufficiently small size (particularly true for ponderosa pine) (Brown and Bevins 1986; van Wagtenonk and Moore 2010). Although our results for small woody fuels were in agreement with those of Fry and Stephens (2010), their finding that pine-dominated plots in a mixed conifer forest also had a lower litter load is contrary to the positive association between pine canopy cover and litter load in this study (Table 2). This difference could be due to differences in fire history or site productivity between study areas. Their site (Sierra San Pedro Martir) has a much more intact fire regime, with fires occurring until at least the early 1970s, and is generally less productive (Stephens and Gill 2005). Both of these factors would lead to lower litter accumulation and perhaps different relationships between stand structure and surface fuels. Our results more closely relate to fuel deposition studies in Yosemite National Park, in which fuel samples collected under ponderosa and sugar pines generally had higher litter and lower 1-h fuel inputs and loads than samples collected under white fir and incense cedar (van Wagtenonk *et al.* 1998; van Wagtenonk and Moore 2010).

Duff was negatively associated with black oak BA, but positively associated with measures of total BA and cover. Other species-specific variables were not important predictors for duff (Table 4). As all of the conifer species at our study site tend to accumulate large quantities of duff in the absence of fire (van Wagtenonk *et al.* 1998), they may have been more similar in their associations with duff load. Hardwood litter tends to decompose more quickly than conifer litter (Harmon *et al.* 1990), potentially contributing to the pattern of lower duff accumulation near oaks. In addition, oaks tend to occur on drier and rockier sites that may be less conducive to conifer establishment (McDonald 1969) and are expected to have lower productivity.

Despite the inclusion of either total or white fir canopy cover in the top predictive model for all fuel components, both of these variables generally had a relatively small range of predictive influence (Fig. 3). A large proportion (45%) of plots had 100% canopy cover, so this likely reflects the additional increases in fuel load that occur due to other structural attributes such as higher BA within a closed canopy area. Total canopy cover tended to influence the level of fuel load below its mean value, whereas white fir canopy cover had more of its influence above the mean prediction level. This may reflect that overall degree of canopy openness influences fuel loads in their lower range of values, but a greater proportion of white fir can contribute to additional fuel load for fine woody fuels.

Live pine BA also had a relatively small range of influence (Fig. 3), despite its high importance for predicting both 1- and



10-h fuels, and it tended to influence fuel loads below their mean value. This implies that the role of pine is most significant when loads of 1- and 10-h fuels are low, and the influence of pine is lost when greater fuel loads are present. In contrast, BA of live fir and total live and dead BA had wide ranges of influence on predicted fuel loads, indicating that these variables are good general predictors of fuel load, even at high values. For example, within the range of values observed for live pine BA, the maximum predicted 1-h fuel load (holding total live BA and white fir CC at their average values) was around  $1 \text{ Mg ha}^{-1}$ , close to the average predicted 1-h fuel load. Conversely, increasing total live BA to its maximum (holding white fir CC and live pine BA at their average values) gives a predicted 1-h fuel load of around  $5 \text{ Mg ha}^{-1}$ , close to the maximum of 5.8 observed in the dataset (Fig. 3).

There are a few limitations in our study that are worth mentioning due to their potential effect on the results reported and their applicability elsewhere. The length of sampling transects may not be optimal for capturing all the variability in surface fuels. Sample length was 3 m for 1–100-h fuels and 10 m for 1000-h fuels. Several studies have found that substantially longer transects are better for adequately characterising fuel loads, particularly for larger size classes (e.g. Sikkink and Keane 2008; Keane and Gray 2013). However, the extent of sampling was similar to or slightly greater than that in other studies using the planar intercept method in Sierra Nevada mixed conifer forests, which typically ranged from 0.01 to 0.06 m of transect per square metre (Innes *et al.* 2006; Webster and Halpern 2010; Stephens *et al.* 2012). Our study used 0.07 m of transect per square metre of plot. Greater transect length would likely have decreased the variability in our measurements and resulted in fewer occurrences of zeroes for the larger fuel classes. Second, all transects were oriented in one direction (east–west). If fuels are not randomly oriented with respect to slope or predominant wind direction this can cause bias in measurements (Batschelet 1981). However, we believe this likely had a minimal effect on our data as sample transects occurred on a variety of slopes and aspects. And last, our findings are from one relatively small (100 ha) study site in the central Sierra Nevada. One of the advantages of the relatively small geographic scope of this study is that we were able to isolate some key within-stand overstorey composition and structure variables that were linked to surface fuel loads, without confounding by factors such as time since past disturbance or site productivity. Although the broader applicability of our findings from this site is unclear, our study site has a management history that is similar to much of the mixed conifer forest in the Sierra Nevada, and is of particular interest for fuels management and restoration. Development of robust predictive linkages applicable across broader geographic scales will require considerable additional sampling in different forest settings, with varying disturbance histories.

### Management implications

Forest surface fuels have high inherent variability, which, as our analyses indicate, are partially tied to small-scale variability in forest overstorey structure and composition. A better understanding of factors associated with variation in fuel loads can be used to help anticipate variation in fire behaviour and effects in

heterogeneous forest environments. For example, we found a positive association between abundance of white fir and greater total fine surface fuel loads. Given that fine fuels are often what drive surface fire behaviour (Rothermel 1972; Albini 1976), pockets of greater fir abundance may experience higher surface fire intensities, and thus more severe fire effects, particularly when burning in mid–late summer when fuel moistures are uniformly low (Bigelow and North 2012). Fuel beds in dense patches with higher overall canopy cover and total BAs would be expected to follow similar trajectories. In areas with very high proportions of white fir, this effect on fire severity may be compounded by its greater sensitivity to fire (Stephens and Finney 2002) and the presence of ladder fuels, a structure that often coincides with white fir dominance. In contrast, breaks in canopy cover were associated with lower fuel loads and may serve to reduce the continuity of surface fuels, thereby affecting the rate and pattern of fire spread.

Another potential application of these study results is to aid in prioritising areas for surface fuel reduction treatments. Altering the overstorey can lead to an immediate input of surface fuels if these are not also removed by the treatment, but resulting changes in overstorey could be expected to alter the fuel inputs and microclimate and thereby alter future fuel accumulation. Our findings highlight structural characteristics with the greatest potential effect on fuel loading, and therefore illustrate forest characteristics that might be manipulated to maximise future fuel heterogeneity and discontinuity. This knowledge could be applied in the design of more heterogeneous fuel treatments. Forest managers are increasingly emphasising restoration of resilient forest conditions that also provide habitat for multiple species of concern with diverse habitat requirements (North *et al.* 2009; North 2012). Management actions that increase overstorey heterogeneity may also lead to greater diversity in surface fuels within stands, which could help to perpetuate a heterogeneous forest structure under the influence of fire. For example, stands that have clustered associations of tree species as opposed to being distributed more uniformly may produce greater diversity in fuel bed characteristics in the future, and would therefore be expected to experience a greater variety of fire effects.

Duff and litter combined comprised nearly two-thirds of the total fuel load sampled (Table 1). Given their magnitude, these duff and litter loads have the potential to disproportionately influence fire behaviour (e.g. intensity, rate of spread [litter]) and effects (e.g. emissions, soil heating [duff], vegetation injury or mortality [both]). Therefore, manipulation of variables associated with these fuel components might be expected to have a greater influence on fuel trajectories, especially since variables that were more strongly associated with duff and litter also had relationships with other fuel components, such as total live BA (high importance values for duff, 1-h, 10-h) and total dead BA (high importance values for 1–100-h fuels and litter). Continued management of a stand following treatment may also have an effect on its future trajectory. Although we do not have post-burn fuel data, we suspect that the relationships we identified with overstorey structure/composition may be more pronounced following low- to moderate-severity fire (i.e. where overstorey trees survive) than those observed after decades of fire exclusion.

## Acknowledgements

We would especially like to thank Jim Baldwin at the USDA Forest Service, Pacific Southwest Research Station for his advice and assistance with statistical analyses. Three anonymous reviewers and the associate editor provided substantial feedback that greatly improved the clarity and applicability of the manuscript. We are also grateful to Ben Weise, Chris Dow, Carolyn Richter, Bob Carlson and Celeste Abbot for their efforts in collecting field data. This work was supported in part by the USDA, National Institute of Food and Agriculture (NIFA) program, grant number 11-03859.

## References

- Agee JK, Skinner CN (2005) Basic principles of forest fuel reduction treatments. *Forest Ecology and Management* **211**, 83–96. doi:10.1016/J.FORECO.2005.01.034
- Albini FA (1976) Estimating wildfire behavior and effects. USDA Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-GTR-30. (Ogden, UT).
- Arroyo LA, Pascual C, Manzanera JA (2008) Fire models and methods to map fuel types: the role of remote sensing. *Forest Ecology and Management* **256**, 1239–1252. doi:10.1016/J.FORECO.2008.06.048
- Bachmann A, Allgower B (2002) Uncertainty propagation in wildland fire behaviour modelling. *International Journal of Geographical Information Science* **16**, 115–127. doi:10.1080/13658810110099080
- Batschelet E (1981) 'Circular Statistics in Biology.' (Academic Press: London)
- Bigelow SW, North MP (2012) Microclimate effects of fuels-reduction and group-selection silviculture: implications for fire behavior in Sierran mixed-conifer forests. *Forest Ecology and Management* **264**, 51–59. doi:10.1016/J.FORECO.2011.09.031
- Brown JK (1974) Handbook for inventorying downed woody material. USDA Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-16. (Ogden, UT).
- Brown JK, Bevins CD (1986) Surface fuel loadings and predicted fire behavior for vegetation types in the northern Rocky Mountains. USDA Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-358. (Ogden, UT).
- Brown JK, See TE (1981) Downed dead woody fuel and biomass in the Northern Rocky Mountains. USDA Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-117. (Ogden, UT).
- Burnham KP, Anderson DR (2002) 'Model Selection and Multi-model Inference: a Practical Information-Theoretic Approach.' (Springer-Verlag: New York)
- Busse MD, Busse MD, Fiddler GO, Shestak CJ, Powers RF (2005) Lethal soil temperatures during burning of masticated forest residues. *International Journal of Wildland Fire* **14**, 267–276. doi:10.1071/WF04062
- Collins BM, Stephens SL (2007) Fire scarring patterns in Sierra Nevada wilderness areas burned by multiple wildland fire use fires. *Fire Ecology* **3**, 53–67. doi:10.4996/FIREECOLOGY.0302053
- Duff TJ, Bell TL, York A (2013) Predicting continuous variation in forest fuel load using biophysical models: a case study in south-eastern Australia. *International Journal of Wildland Fire* **22**, 318–332. doi:10.1071/WF11087
- Dunning D (1942) A site classification for the mixed-conifer selection forests of the Sierra Nevada. USDA Forest Service, California Forest and Range Experiment Station, Research Note 28. (Berkeley, CA).
- Fernandes PM (2009) Combining forest structure data and fuel modelling to classify fire hazard in Portugal. *Annals of Forest Science* **66**, 415–424. doi:10.1051/FORREST/2009013
- Fonda RW (2001) Burning characteristics of needles from eight pine species. *Forest Science* **47**, 390–396.
- Fonda RW, Varner JM (2004) Burning characteristics of cones from eight pine species. *Northwest Science* **78**, 322–333.
- Fonda RW, Belanger LA, Burley LL (1998) Burning characteristics of western conifer needles. *Northwest Science* **72**, 1–9.
- Freckleton RP (2011) Dealing with collinearity in behavioural and ecological data: model averaging and the problems of measurement error. *Behavioral Ecology and Sociobiology* **65**, 91–101. doi:10.1007/S00265-010-1045-6
- Fry DL, Stephens SL (2010) Stand-level spatial dependence in an old-growth Jeffrey pine–mixed conifer forest, Sierra San Pedro Martir, Mexico. *Canadian Journal of Forest Research* **40**, 1803–1814. doi:10.1139/X10-122
- Gabrielson AT, Larson AJ, Lutz JA, Reardon JJ (2012) Biomass and burning characteristics of sugar pine cones. *Fire Ecology* **8**, 58–70. doi:10.4996/FIREECOLOGY.0803058
- Ganteaume A, Lampin-Maillet C, Guijarro M, Hernando C, Jappiot M, Fonturbel T, Perez-Gorostiaga P, Vega JA (2009) Spot fires: fuel bed flammability and capability of firebrands to ignite fuel beds. *International Journal of Wildland Fire* **18**, 951–969. doi:10.1071/WF07111
- Hall SA, Burke IC, Hobbs NT (2006) Litter and dead wood dynamics in ponderosa pine forests along a 160-year chronosequence. *Ecological Applications* **16**, 2344–2355. doi:10.1890/1051-0761(2006)016[2344:LADWDI]2.0.CO;2
- Harmon ME, Baker GA, Spycher G, Greene SE (1990) Leaf-litter decomposition in the Picea/Tsuga forests of Olympic National Park, Washington, U.S.A. *Forest Ecology and Management* **31**, 55–66. doi:10.1016/0378-1127(90)90111-N
- Hille MG, Stephens SL (2005) Mixed conifer forest duff consumption during prescribed fires: tree crown impacts. *Forest Science* **51**, 417–424.
- Hothorn T, Hornik K, Zeileis A (2006) Unbiased recursive partitioning: a conditional inference framework. *Journal of Computational and Graphical Statistics* **15**, 651–674. doi:10.1198/106186006X133933
- Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* **54**, 187–211. doi:10.2307/1942661
- Hurvich CM, Tsai CL (1989) Regression and time-series model selection in small samples. *Biometrika* **76**, 297–307. doi:10.1093/BIOMET/76.2.297
- Innes JC, North MP, Williamson N (2006) Effect of thinning and prescribed fire restoration treatments on woody debris and snag dynamics in a Sierran old-growth, mixed-conifer forest. *Canadian Journal of Forest Research* **36**, 3183–3193. doi:10.1139/X06-184
- Jakubowski MK, Guo Q, Collins B, Stephens S, Kelly M (2013) Predicting surface fuel models and fuel metrics using Lidar and CIR imagery in a dense, mountainous forest. *Photogrammetric Engineering and Remote Sensing* **79**, 37–49. doi:10.14358/PERS.79.1.37
- Johnson JB, Omland KS (2004) Model selection in ecology and evolution. *Trends in Ecology & Evolution* **19**, 101–108. doi:10.1016/J.TREE.2003.10.013
- Keane RE (2008a) Surface fuel litterfall and decomposition in the northern Rocky Mountains, U.S.A. USDA Forest Service, Rocky Mountain Research Station, Research Paper RMRS-RP-70. (Fort Collins, CO).
- Keane RE (2008b) Biophysical controls on surface fuel litterfall and decomposition in the northern Rocky Mountains, USA. *Canadian Journal of Forest Research* **38**, 1431–1445. doi:10.1139/X08-003
- Keane RE (2013) Describing wildland surface fuel loading for fire management: a review of approaches, methods and systems. *International Journal of Wildland Fire* **22**, 51–62. doi:10.1071/WF11139
- Keane RE, Gray K (2013) Comparing three sampling techniques for estimating fine woody down dead biomass. *International Journal of Wildland Fire* **22**, 1093–1107. doi:10.1071/WF13038
- Keane RE, Burgan R, van Wagendonk J (2001) Mapping wildland fuels for fire management across multiple scales: integrating remote sensing, GIS, and biophysical modeling. *International Journal of Wildland Fire* **10**, 301–319. doi:10.1071/WF01028

- Keane RE, Gray K, Bacciu V (2012a) Spatial variability of wildland fuel characteristics in northern Rocky Mountain ecosystems. USDA Forest Service, Rocky Mountain Research Station, Research Paper RMRS-RP-98. (Fort Collins, CO).
- Keane RE, Gray K, Bacciu V, Leirfallom S (2012b) Spatial scaling of wildland fuels for six forest and rangeland ecosystems of the northern Rocky Mountains, USA. *Landscape Ecology* **27**, 1213–1234. doi:10.1007/S10980-012-9773-9
- Keifer M, Van Wagtenonk JW, Buhler M (2006) Long-term surface fuel accumulation in burned and unburned mixed-conifer forests of the central and southern Sierra Nevada, CA USA. *Fire Ecology* **2**, 53–72. doi:10.4996/FIREECOLOGY.0201053
- Kittredge J (1955) Some characteristics of forest floors from a variety of forest types in California. *Journal of Forestry* **53**, 645–647.
- Knapp EE, Keeley JE (2006) Heterogeneity in fire severity within early season and late season prescribed burns in a mixed-conifer forest. *International Journal of Wildland Fire* **15**, 37–45. doi:10.1071/WF04068
- Knapp EE, North M, Benech M, Estes BL (2012) The variable-density thinning study at Stanislaus–Tuolumne experimental forest. In ‘Managing Sierra Nevada forests. USDA Forest Service, Pacific Southwest Research Station General Technical Report PSW-GTR-237.’ (Ed. M North.) pp. 127–139. (Albany, CA)
- Knapp EE, Skinner CN, North MP, Estes BL (2013) Long-term overstory and understory change following logging and fire exclusion in a Sierra Nevada mixed-conifer forest. *Forest Ecology and Management* **310**, 903–914. doi:10.1016/J.FORECO.2013.09.041
- Lundquist JE (2007) The relative influence of diseases and other small-scale disturbances on fuel loading in the black hills. *Plant Disease* **91**, 147–152. doi:10.1094/PDIS-91-2-0147
- McDonald PM (1969) Silvical characteristics of California black oak (*Quercus kelloggii* Newb.). USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, Research Paper RP-PSW-053. (Berkeley, CA).
- Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining  $R^2$  from generalized linear mixed-effects models. *Methods in Ecology and Evolution* **4**, 133–142. doi:10.1111/J.2041-210X.2012.00261.X
- North MP (2012) Managing Sierra Nevada forests. USDA Forest Service, Pacific Southwest Research Station, General Technical Report PSW-GTR-237. (Albany, CA).
- North MP, Stine P, Zielinski W, Stephens S (2009) An ecosystem management strategy for Sierran mixed-conifer forests. USDA Forest Service, Pacific Southwest Research Station, General Technical Report PSW-GTR-220. (Albany, CA).
- Ottmar RD, Blake JJ, Crollly WT (2012) Using fine-scale fuel measurements to assess wildland fuels, potential fire behavior and hazard mitigation treatments in the southeastern USA. *Forest Ecology and Management* **273**, 1–3. doi:10.1016/J.FORECO.2011.11.003
- Parresol BR, Blake JJ, Thompson AJ (2012) Effects of overstory composition and prescribed fire on fuel loading across a heterogeneous managed landscape in the southeastern USA. *Forest Ecology and Management* **273**, 29–42. doi:10.1016/J.FORECO.2011.08.003
- R Core Team (2013) ‘A language and environment for statistical computing.’ (R Foundation for Statistical Computing: Vienna)
- Rocca ME (2009) Fine-scale patchiness in fuel load can influence initial post-fire understory composition in a mixed conifer forest, Sequoia National Park, California. *Natural Areas Journal* **29**, 126–132. doi:10.3375/043.029.0204
- Rothermel RC (1972) A mathematical model for predicting fire spread in wildland fuels. USDA Forest Service, Intermountain Forest and Range Experiment Station, Research Paper RP-INT-115. (Ogden, UT).
- SAS Institute Inc (2011) ‘SAS 9.3.’ (SAS Institute Inc.: Cary, NC)
- Scott JH, Reinhardt ED (2001) Assessing crown fire potential by linking models of surface and crown fire behavior. USDA Forest Service, Rocky Mountain Research Station, Research Article RMRS-RP-29. (Fort Collins, CO).
- Sikkink PG, Keane RE (2008) A comparison of five sampling techniques to estimate surface fuel loading in montane forests\*. *International Journal of Wildland Fire* **17**, 363–379. doi:10.1071/WF07003
- Smith TF, Rizzo DM, North M (2005) Patterns of mortality in an old-growth mixed-conifer forest of the southern Sierra Nevada, California. *Forest Science* **51**, 266–275.
- Stephens SL, Finney MA (2002) Prescribed fire mortality of Sierra Nevada mixed conifer tree species: effects of crown damage and forest floor combustion. *Forest Ecology and Management* **162**, 261–271. doi:10.1016/S0378-1127(01)00521-7
- Stephens SL, Gill SJ (2005) Forest structure and mortality in an old-growth Jeffrey pine–mixed conifer forest in north-western Mexico. *Forest Ecology and Management* **205**, 15–28. doi:10.1016/J.FORECO.2004.10.003
- Stephens SL, Finney MA, Schantz H (2004) Bulk density and fuel loads of ponderosa pine and white fir forest floors: impacts of leaf morphology. *Northwest Science* **78**, 93–100.
- Stephens SL, Collins BM, Roller G (2012) Fuel treatment longevity in a Sierra Nevada mixed conifer forest. *Forest Ecology and Management* **285**, 204–212. doi:10.1016/J.FORECO.2012.08.030
- Stohlgren TJ (1988) Litter dynamics in 2 Sierran mixed conifer forests. 1. Litterfall and decomposition rates. *Canadian Journal of Forest Research* **18**, 1127–1135. doi:10.1139/X88-174
- Thaxton JM, Platt WJ (2006) Small-scale fuel variation alters fire intensity and shrub abundance in a pine savanna. *Ecology* **87**, 1331–1337. doi:10.1890/0012-9658(2006)87[1331:SFVAFI]2.0.CO;2
- van Wagtenonk JW, Moore PE (2010) Fuel deposition rates of montane and subalpine conifers in the central Sierra Nevada, California, USA. *Forest Ecology and Management* **259**, 2122–2132. doi:10.1016/J.FORECO.2010.02.024
- van Wagtenonk JW, Sydoriak CA (1987) Fuel accumulation rates after prescribed fires in Yosemite National Park. In ‘Ninth Conference on Fire and Forest Meteorology, American Meteorological Society’, 21–24 August 1987, San Diego, CA. (Eds JW van Wagtenonk, CA Sydoriak) pp. 101–105 (American Meteorology Society: Boston, MA)
- van Wagtenonk JW, Benedict JM, Sydoriak WM (1996) Physical properties of woody fuel particles of Sierra Nevada conifers. *International Journal of Wildland Fire* **6**, 117–123. doi:10.1071/WF9960117
- van Wagtenonk JW, Benedict JM, Sydoriak WM (1998) Fuel bed characteristics of Sierra Nevada conifers. *Western Journal of Applied Forestry* **13**, 73–84.
- Wagner CV (1977) Conditions for the start and spread of crown fire. *Canadian Journal of Forest Research* **7**, 23–34. doi:10.1139/X77-004
- Weatherspoon CP, Skinner CN (1995) An assessment of factors associated with damage to tree crowns from the 1987 wildfires in northern California. *Forest Science* **41**, 430–451.
- Webster KM, Halpern CB (2010) Long-term vegetation responses to reintroduction and repeated use of fire in mixed-conifer forests of the Sierra Nevada. *Ecosphere* **1**, art9. doi:10.1890/ES10-00018.1