Scaling from leaf traits to fire behaviour: community composition predicts fire severity in a temperate forest

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Summary

1. Although species differ in flammability, identifying the traits that influence flammability and linking them to other axes of trait variation has yet to be accomplished. Leaf length may be a key trait influencing the flammability of leaf litter.

2. Differences in species composition across a landscape or changes in composition through time may alter fire behaviour. Forests in the Sierra Nevada of CA, USA, have experienced changes in species composition that have modified the distribution of leaf litter traits.

3. Across three independent data sets, at scales from a single watershed to multiple watersheds and elevations, we tested if mean community leaf length in patterns of fire severity. We used structural equation models to disentangle direct effects of site characteristics from the contribution of species composition.

4. Fire severity was greater at sites inhabited by species with longer leaves than at sites containing short-leaved species, probably as a result of lower litter density. The effect cannot be explained merely by the joint influence of site characteristics on both fire behaviour and species composition.

5. A significant portion of this pattern is driven by shifts in the abundance of *Pinus* species. In this system, pines are among the longest-leaved species and this makes it difficult to separate leaf-length effects from other possible flammability-enhancing characteristics of pines. Evidence from one data set, however, suggests that the pattern cannot be entirely explained by proportion of pines alone.

6. *Synthesis*. We demonstrate that a simple integration of a species trait predicts fire severity at landscape scales. This provides a link between the two scales at which most previous work has occurred: species-specific measurements of traits and landscape-level characterisation of fuel loads. Investigations of trait effects on fire behaviour are important because climate change may lead to novel climates and no-analogue species assemblages. In this ecosystem, shorter-leaved species, which have increased in density during the period of fire exclusion, may act as a positive feedback by reducing fire severity and thereby favouring their own establishment. Conversely, restoration of fire to these forests, by increasing the dominance of long-leaved species, may increase flammable fuels.

Key-words: determinants of plant community diversity and structure, fire regime, flammability, functional traits, leaf length, litter, plant population and community dynamics, Sierra Nevada, species distributions

Introduction

The search for general rules linking species and environmental conditions has been central to community ecology (Grime 1979; Southwood 1988). Although much past work focused on categorizing species into discrete groups ('functional groups', Lavorel *et al.* 1997), a more recent trend has been the use of quantitative continuous traits to predict how species may respond to the environment and to predict how species composition will affect ecosystem processes (Díaz & Cabido 2001; Lavorel & Garnier 2002). Prompted especially by the need to predict ecosystem responses to global change, researchers have shown increasing interest in linking characteristics of individual species to their effects on ecosystem-level properties (Lavorel *et al.* 1997; Grime 2001; Lavorel & Garnier 2002; Garnier *et al.* 2004; Violle *et al.* 2007; Cornwell *et al.* 2008). Fire is a

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globally important ecosystem process (Bond, Woodward & Midgley 2005), but our ability to link fire behaviour to plant traits is still rudimentary. The study of how leaf traits influence litter flammability has the potential to link an important ecological process, fire, with increasingly well-studied suites of plant traits related to species distributions and community assembly (Westoby *et al.* 2002; Wright *et al.* 2004). A trait-based approach has the potential to offer both better explanation and prediction than static classifications of vegetation as fuel. Such an approach may be especially useful as plant community composition shifts under ongoing global change (McGill *et al.* 2006).

Although it is acknowledged that species differ in flammability (Philpot 1977; van Wilgen, Higgins & Bellstedt 1990; van Wagtendonk, Benedict & Sydoriak 1996; Dimitrakopoulos 2001; Behm *et al.* 2004), the process of identifying functional traits that influence flammability is still in an early stage. Landscape-scale analyses have found variation in species composition to be an indicator of past and current fire regimes (Kellman 1984; Beaty & Taylor 2001; Bekker & Taylor 2001; Blarquez, Bremond & Carcaillet 2010; Odion, Moritz & Della-Sala 2010), but the actual scaling from plant traits to fire behaviour has proved more elusive. Different plant traits may be important to different aspects of flammability, and traits important for crown fire behaviour will differ from those important in litter-driven surface fires. In semi-arid climates with low decomposition rates, litter accumulation is high and surface fuels (such as leaf litter) are important for fire transmission (Bradstock & Cohn 2002). In many forests, leaf litter constitutes the most substantial component of total litter floor (e.g. Kauffman, Cummings & Ward 1994; Sundarapandian & Swamy 1999; Dearden *et al.* 2006). Leaf litter flammability may be an example of leaf traits involved in growth and defence continuing to have ecosystem consequences after they senesce and fall – similar to the 'afterlife' effect of green leaf traits on decomposition (Cornwell *et al.* 2008). Understanding how leaf traits influence fire has the potential to link fire behaviour to a wider range of correlated leaf traits relative to habitat preference, water use niches and successional stage (Wright *et al.* 2004).

Lab-based experimental burning of reconstructed litter samples has demonstrated that leaf arrangement and morphology can influence flammability (Bradstock & Cohn 2002; Scarff & Westoby 2006; Kane, Varner & Hiers 2008; Plucinski & Anderson 2008). Litter density is an important factor in controlling litter flammability (e.g. Plucinski & Anderson 2008) and leaf size and shape can influence packing density. Larger and longer leaves (Scarff & Westoby 2006) and leaves with lobes (Kane, Varner & Hiers 2008) produce low-density, better-ventilated litter beds. Reconstructed litter beds, however, use relatively fresh, undecomposed leaf litter. The actual litter density and ventilation in nature will depend not only on the original size and shape of leaves, but also on the rate at which the leaves decompose. To measure litter flammability under more natural conditions, Ganteaume *et al.* (2009a,b), have conducted experimental fires of intact litter beds and shown that vegetation type can influence important flammability

characteristics. Together, these studies suggest that leaf length, by influencing litter bed density and ventilation, may affect fire behaviour.

Among species with similar leaf decomposition rates, larger or longer leaves should produce lower-density litter (Scarff & Westoby 2006). Across a wider range of species and forest types, leaf length alone may not predict litter particle sizes. Species differ in decomposition rates due to moisture, carbon : nitrogen ratios and lignin content, and large leaves (especially those with low leaf area per mass) may have faster decomposition rates (Cornwell *et al.* 2008) and therefore create denser rather than lighter litter. Nevertheless, in semi-arid systems and among species with leaves of relatively similar chemistry, leaf length may be a good predictor of litter packing. We examined leaf length as a possible predictor of fire severity in litter-driven fires in montane forests in mediterranean-climate California.

Frequent fire is a major ecosystem influence in California's Sierra Nevada forests (Swetnam & Baisan 2003). Introduction of grazing, decimation of the Native American population, and more recent fire suppression policies have together excluded fire since *c.* 1860. The effect of fire exclusion that has caused the most interest and alarm is the increase in tree density and the concurrent increase in ladder fuels, but another important effect of fire exclusion has been the change in community composition. Fire exclusion has altered stand composition by allowing shade-tolerant species such as *Abies* to increase relative to shade-intolerant species such as *Pinus* (Parsons & DeBennedetti 1979; Barbour *et al.* 2002). A consequence of these changes in species composition has been a shift in the distribution of leaf lengths: forests once dominated by long-needled *Pinus* are now increasingly dominated by short-needled *Abies*. The litter from these species may differ in flammability as a consequence of how aerated the litter is on the forest floor. Among Sierran conifer species, litter bulk density varies much more than does heat content of the litter material (van Wagtendonk, Benedict & Sydoriak 1998a,b). We ask, can an ecosystem-level property (fire severity) be predicted by integrating the community-wide distribution of a single plant trait (Violle *et al.* 2007)? We explore a very simple integration function: mean community leaf length. Our prediction is that increased leaf length, by decreasing litter bulk density, should increase litter flammability and local fire severity.

We investigated variation in species composition within a forest. This variation in composition results from past disturbance history and landscape-scale habitat heterogeneity along environmental gradients such as aspect and elevation. Many environmental variables are likely to jointly influence species distributions as well as fire behaviour. Therefore, any investigation of possible community composition effects on fire severity must account for such factors jointly influencing species' distributions and fire behaviour. We used structural equation modelling (also known as 'modern path analysis' Grace 2006) to test for a causal effect of community composition (represented as mean community leaf length) on observed fire severity. We tested our model in three independent data sets to determine if any association between mean leaf length and fire

severity is best explained by the joint effect of spatial environmental factors or by a direct causal path from mean leaf length to fire severity. We hypothesized that mean community leaf length positively influences local fire severity.

Materials and methods

We tested the hypothesis that community composition influences fire severity in three independent data sets at three different spatial scales. We use the term 'fire severity' as recommended by Keeley (2009): post-fire measurements of organic material loss and tissue damage as estimates of fire intensity a site experienced (or, in the case of one data set, we use measures of fire damage to trees). In these forests, such measurements of fire severity are good predictors of ecosystem response to fire (Knapp & Keeley 2006; Schwilk *et al.* 2006). Each of these data sets included plot-based post-fire measurements of fire severity and estimates of pre-fire community composition within forest vegetation in Sequoia and Kings Canyon National Parks, CA, USA (36°36′N, 118°42′W, Fig. 1). These three data sources are

outlined in Table 1 and are described in detail below. The Fire and Fire Surrogate (FFS) and Fire Effects (FE) data include only prescribed fires, while the Composite Burn Index (CBI) data includes some wild fires at higher elevations. Prescribed fires were conducted according to prescription outlines in the Sequoia and Kings Canyon Fire and Fuels Management Plan (http://www.nps.gov/seki/nature science/fic_ffmp.htm).

DATA SOURCES

Fire and Fire Surrogate Study

The Sequoia National Park Fire and Fire Surrogate (FFS) study was a replicated experiment testing the ecological effects of early and late-season burning (Table 1). The study included six replicated experimental units each 11–20 ha in size (three early summer and three late-season fires; we exclude data from unburned control units in this analysis), with pre and post-fire data from ten 0.1-ha vegetation plots within each unit. This was the smallest-scale data set included; it was restricted to a single slope above Wolverton Creek and it included a
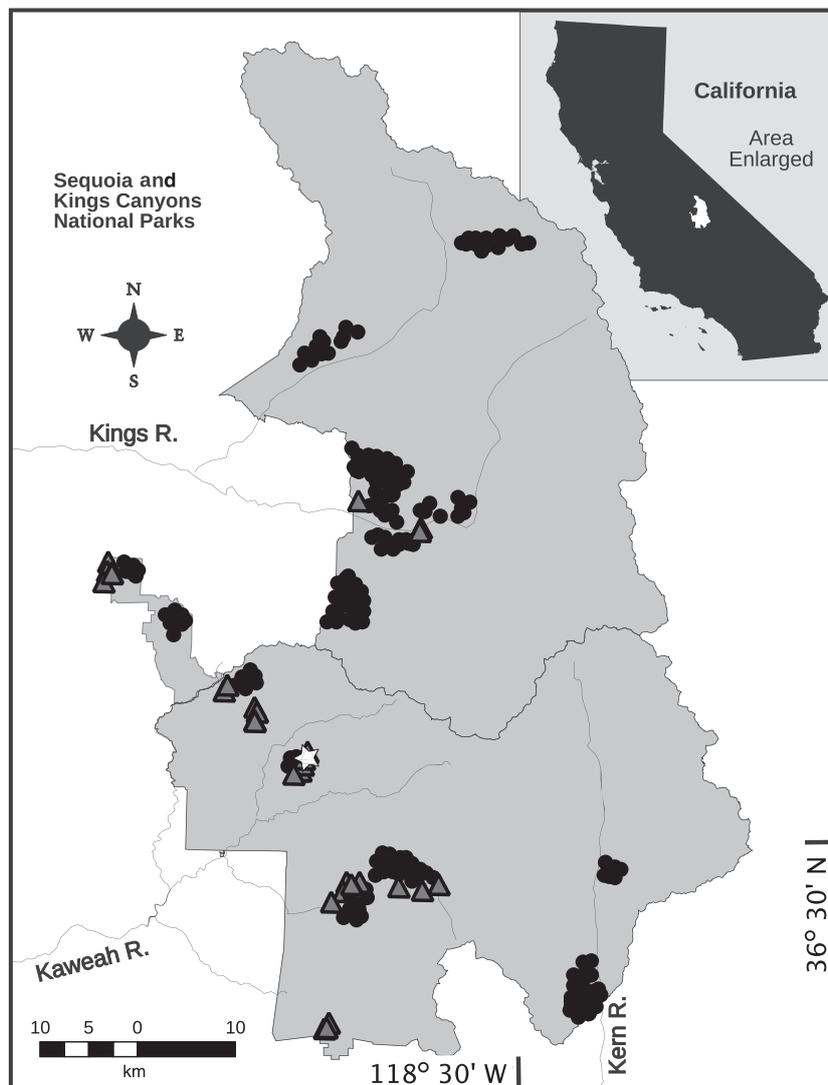

Fig. 1. Map showing the outline of Sequoia and Kings Canyon National Parks, the location of the Fire and Fire Surrogate Plots (star symbol, individual plots not shown due to scale), the Fire Effects (FE) plots (open triangles) and the Composite Burn Index (CBI) plots (closed circles).

Table 1. Three independent data sources were used in this study. The table indicates scale, primary vegetation type, elevation range and sample size for each data source. Fire types are indicated as wild fire or prescribed fire (Rx)

Data source	Scale	Vegetation type	Fire types	Elevation	*N*
Fire and Fire Surrogate (FFS)	Partial watershed	Mixed conifer	Rx	2000 m	60
Fire Effects (FE)	Multiple watersheds	Mixed conifer	Rx	2000 m	29
Composite Burn Index (CBI)	Multiple watersheds	Multiple forest types	Wild fire and Rx	1000–3000 m	344

narrow range of elevation (1900–2150 m a.s.l.) on a north-west aspect. These data represent a relatively small spatial scale with subtle composition differences among plots: all plots are mixed conifer forest and differ primarily in the relative abundance of species rather than in large shifts in species presence/absence. The late-season prescribed fires were conducted in September and October 2001, the early season fires in June 2002. The study and methods are described in detail in Knapp & Keeley (2006); Schwilk *et al.* (2006) and Knapp *et al.* (2007). For the current analyses, each 0.1-ha plot was used as an individual data point. Spatial autocorrelation in fire severity measures was low (van Mantgem & Schwilk 2009). All trees in the 0.1-ha plots were tagged and diameter at 1.37 m height was measured prior to the fires. Therefore, these data include accurate pre-fire measurements of stand composition weighted by basal area.

For this data set, we used the geometric mean of crown scorch height and bole char height as the measure of fire severity because it is a good predictor of tree mortality in the FFS study and was available at the plot level (Schwilk *et al.* 2006). Past work has shown that season has a significant effect on fire severity but that the effect is of small magnitude in this system with late-season fires having mean crown scorch-bole char heights of 1.6 m higher than early season burns (Schwilk *et al.* 2006). To account for seasonality effects when combining all units into a single analysis, we transformed our fire severity measure by using the residuals of the linear model describing geometric mean crown scorch and bole char height as a function of season of burn – this effectively reduced values in late-season burns by 1.6 m.

National Park Service Fire Effects plots

This multiple watershed data set consists of FE plots located within prescribed fire boundaries in the mixed conifer forest of Sequoia and Kings Canyon National Parks. These are permanent plots, established since 1982, to monitor both short- and long-term effects of prescribed fires and to provide information to resource managers (USDI National Park Service 2003). The prescribed fires were conducted primarily during late season (September and October) to mimic naturally occurring fires. Individual fires burned over several days and across a wide range of weather conditions. Plots were located in *Pinus ponderosa* mixed conifer, *Abies concolor* mixed conifer, *Sequoiadendron giganteum* mixed conifer, and *Abies magnifica*-dominated forest communities. Plots (0.1 ha) were randomly located pre-fire and stratified across vegetation types with data collected on surface fuels (using Brown's transects, Brown, Oberheu & Johnston 1982), understorey species cover, overstorey tree species, seedling density and fire severity. All standing trees (live and dead) > 1.4 m tall were tagged and diameters recorded pre and post-fire. Plots were sampled pre-fire and immediately post-fire. Fire severity was measured as the combined total depth of litter and duff consumed.

National Park Service Composite Burn Index plots

The largest-scale data set was the CBI plots. These plots were implemented originally to validate Differential Normalized Burn Ratio

(dNBR) data derived from Landsat imagery taken pre-fire and 1 year later following the fires. The ground-based measures of fire severity we used were collected as part of the national extended assessment protocol (Key & Benson 2006). Sampling began in 2003 (on 2002 fires) in Sequoia and Kings Canyon. These plots comprise the largest spatial scale and elevation range across the parks. Circular plots, 30 m in diameter, were randomly located but stratified within five severity classes in each fire based on satellite dNBR values. Following the fire, a visual classification of fire effects was made on substrate, herbaceous plants and low shrubs, tall shrubs and small trees, intermediate trees and large trees. Unlike the other two data sets, the CBI data included forest types outside the mixed conifer zone with CBI plots ranging from low-elevation forests dominated by *P. ponderosa* to sub-alpine woodlands. These plots also had the coarsest estimates of pre-fire species composition because they lacked pre-fire sampling: pre-fire composition was estimated from live and dead material post-fire. Species were assigned importance classes per plot and these corresponded to broad percentage basal area categories. For our analyses, we converted these classes back to estimates of relative basal area in order to obtain a weighted average leaf length per plot. We used the ground-based fire severity score in our analysis and did not use any satellite-derived data.

TRAIT DATA AND ENVIRONMENTAL VARIABLES

We collected leaf traits for each of the 19 most common tree and large shrub species found in the three data sets (> 97% of the basal area contribution over all communities). Traits were collected from plants in a subset of plots in summer 2009. Plots for trait sampling were selected randomly stratifying across fires while excluding plots with an estimated travel time of greater than 2 hours from an access road. Leaves were sampled from a total of 43 plots. In each plot, two individuals per species were sampled with three leaves or needle bunches sampled per individual. For tall species, recently fallen branches were often used to collect still-green dead leaves. A total of 183 individuals were sampled.

We collected mature leaves into plastic bags and transported these to the lab for scanning with a flatbed scanner. Leaf lengths, widths and areas were calculated with Lamina software (Bylesjö *et al.* 2008). For Cupressaceae species (*Calocedrus*, *Juniperus* and *Sequoiadendron*), branchlet length was used instead of leaf length. For these species, freshly fallen litter was used as the branchlet sample with length taken as the longest axis across the generally flattened branchlet.

Species included were *Abies concolor*, *Abies magnifica*, *Arctostaphylos patula*, *Calocedrus decurrens*, *Ceanothus integerrimus*, *Chrysolepis sempervirens*, *Cornus nuttallii*, *Juniperus occidentalis*, *Sambucus mexicana*, *Pinus contorta*, *Pinus jeffreyi*, *Pinus lambertiana*, *Pinus monticola*, *Pinus ponderosa*, *Populus tremuloides*, *Quercus chrysolepis*, *Quercus kelloggii*, *Sequoiadendron giganteum* and *Umbellularia californica*. See Table S1 in Supporting Information for mean leaf lengths.

Weighted average leaf lengths were assigned to plots in each data set according to mean species leaf length and the pre-fire relative basal

area of each species in the plot. For the FFS and FE plots, exact basal area by species was recorded, for the CBI data set, pre-fire relative basal area was predicted from cover class categories measured. For the FE and CBI plots, only tree species were recorded, so average leaf lengths were calculated using only trait data from the 15 tree species: *A. concolor*, *A. magnifica*, *C. decurrens*, *C. nuttallii*, *J. occidentalis*, *P. contorta*, *P. jeffreyi*, *P. lambertiana*, *P. monticola*, *P. ponderosa*, *P. tremuloides*, *Q. chrysolepis*, *Q. kelloggii*, *S. giganteum*, and *U. californica*.

We calculated a suite of environmental variables from plot geographic position. The centre of each plot in all three data sets was projected onto a 10-m-resolution digital elevation model for the region and a suite of derived variables were calculated from the digital elevation model using ESRI ArcMap and Spatial Analyst. Elevation, locally averaged slope and total annual solar radiation were calculated for each point. Relative slope position was also calculated but was neither associated with species composition nor with fire severity and was not used in further analyses.

Although these data sets were originally collected for diverse purposes, each provided a measurement of fire severity. In cases where a data set offered multiple choices for fire severity measures, analysis of data correlation structure guided variable choice. For the FFS data set, our measure was the geometric mean of crown scorch height and bole char height. This measure has been shown to correlate well with fuel consumption and to be a good predictor of tree mortality in this study (Schwilk *et al.* 2006). For the FE data set, our measurement was total depth of litter and duff consumed per plot – for mixed conifer forest, this measure is a good predictor of community response (Knapp & Keeley 2006; Knapp *et al.* 2007). For the CBI data set, the measure was the mean plot-based fire severity score ('ptmean' Key & Benson 2006), a relative score averaging ground fuel consumption and tree scorch scores. This score is an average of five separate severity scores on a 0–3 scale, one for each vegetation stratum: 'substrates', 'herbs, low shrubs and trees less than 1 m', 'tall shrubs and trees 1–5 m', 'intermediate trees', and 'large trees'. Each of these strata scores are, in turn, based on 4–5 visually assessed measurements such as 'percentage canopy mortality'.

ANALYSES

We constructed observed variable structural equation models (SEM) to investigate causal relationships between community composition and fire behaviour (Grace 2006). This framework allows us to account for joint effects of environmental variables on both community composition and fire behaviour as well as test for a causal link of special interest: an effect of community-weighted average leaf length on a fire severity measure. Elevation, plot slope and total annual solar radiation are likely to be correlated with fire severity, but we wanted to know if all or a portion of this effect was best explained by the effect of these environmental variables on species composition.

We examined two classes of models representing alternative hypotheses for each data set (Fig. 2): in Model A, the environmental variables were allowed direct effects on average community leaf length and on fire severity but there was no path between leaf length and fire severity. In Model B, we allowed an additional causal pathway between average leaf length and fire severity (represented by the dashed arrow in Fig. 2). We ran analyses separately for each class of models for each data set and used the 'sem' module (Fox 2006) for R (http://www.R-project.org). In each class non-significant paths (at $P > 0.1$) were removed until a best-fit model was obtained. We chose to use a more conservative than $P = 0.05$ criterion for removing paths because (i) knowledge of the system suggested that these envi-
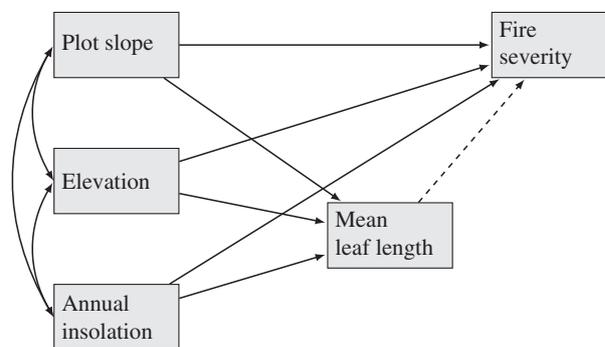

Fig. 2. Alternative models A and B. Model A includes all paths except for dotted line, Model B includes dotted line indicating causal path from leaf length to fire severity. Single-headed arrows represent directed relationships and two-headed arrows indicate unresolved correlations. Residual variances for all observed variables were included in analyses, but are omitted from the figure.

ronmental variables should influence community composition and fire severity and (ii) by leaving environmental variables of marginal predictive power in the model, we allowed the environmental variables to explain a greater amount of the variation in the data and therefore reduce the probability that we would discover a direct leaf-length effect. These alternative models A and B are nested, therefore we were able to compare the relative improvement in model fit obtained by adding the path between leaf length and fire severity by testing chi-square differences and report actual *P*-values. In cases where adding the new path in model B would suggest that other previously significant paths should drop out, we left these paths in place to allow single degree of freedom comparisons between models A and B. Data were transformed to meet modelling assumptions: variables were mean-centred, percentages were arcsine-square-root-transformed, and leaf length was log-transformed.

The CBI data set included forest types outside of the mixed conifer forest that comprised the other two data sets. To allow better comparison with the FFS and FE data, we conducted two additional analyses: one in which we restricted the CBI data only to plots in mixed conifer forest (defined as 1800 m < 2400 m) and a second in which we restricted the analysis to only prescribed fires.

We treated plots as independent, but explicitly included environmental factors as predictors that vary spatially and used nearest-neighbour plots as a spatial autocorrelation proxy. Previous work in these forests has shown spatial autocorrelation in fire effects to be weak (van Mantgem & Schwilk 2009) and patch-scale heterogeneity in fire severity, as measured by scorch heights and area burned, to be quite high (Knapp & Keeley 2006). Distances between plots were smallest in the FFS data set, but previous analysis of this data set using spatial generalized least-squares regression showed no improvement over non-spatial models for fuel consumption and fire severity variables (van Mantgem & Schwilk 2009). In building the 'A' versions of each model, we tested for a spatial autocorrelation not captured by our environmental variables by including nearest-neighbour fire severity as an additional causal variable on fire severity as suggested in Grace (2006) as a method for dealing with potential spatial autocorrelation. In all three data sets, this variable dropped out as an insignificant path and did not appear in the best-fit models.

In these data sets, the phylogenetic structure of communities is confounded with mean leaf length: community mean leaf length is correlated with percentage contribution of pines to basal area (FFS data, $r = 0.88$, FE data $r = 0.57$). Although we cannot fully untangle

these correlated characteristics in these data, we did explore this further by examining alternative models: for each model B investigated, we also tested a model in which mean leaf length was replaced by percentage basal contribution of pines.

Results

RELATIONSHIP BETWEEN LEAF LENGTH AND LITTER BULK DENSITY

For eleven tree species for which litter bulk density has already been measured by van Wagtendonk, Benedict & Sydoriak (1998a), our leaf length measurements showed that leaf length is negatively correlated with bulk density ($r = 0.82$, $P = 0.002$), and therefore is a good candidate as a predictor of local fire severity. The van Wagtendonk, Benedict & Sydoriak (1998a) data were collected on trees at Yosemite National Park

c. 140 km north of the populations from which we sampled leaves.

Data collected from the FFS and FE plots showed that the mean leaf length of the community predicted fire severity (Fig. 3). In the FE data, this relationship existed even after accounting for the proportion of pines in each plot ($r^2 = 0.16$, $P = 0.019$, Fig. 3). Without accounting for environmental variables (as we did in the analyses below), we cannot exclude that environmental factors jointly influence leaf length and fire severity.

OBSERVED VARIABLE MODELS

For the FFS data set, Model B showed strong support over Model A (Table 2, Fig. 4a): there was evidence of a causal path linking average community leaf length with our measure of fire
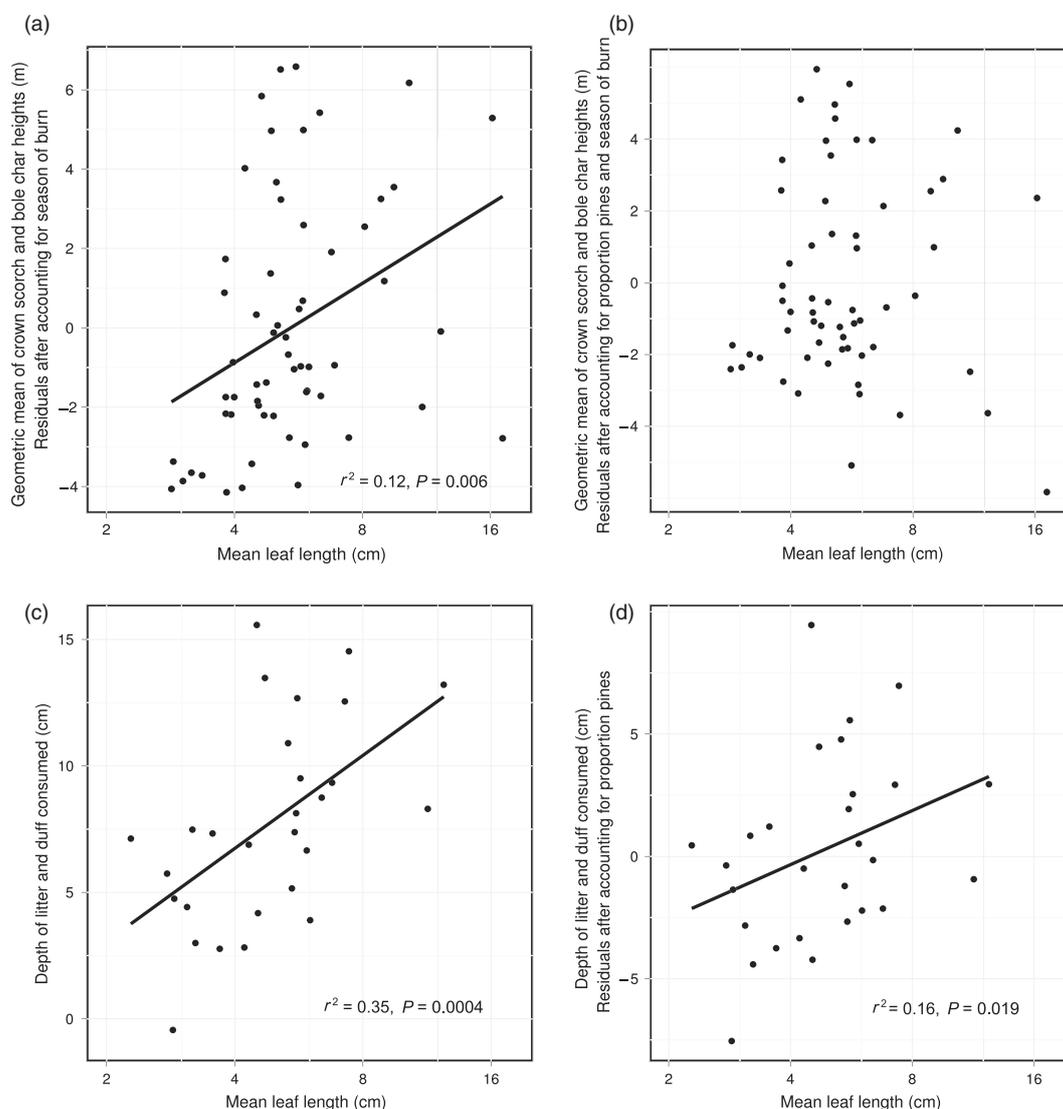

Fig. 3. Mean leaf length and fire severity in the Fire and Fire Surrogate (FFS) and Fire Effects (FE) data. (a) FFS plots: effect of mean leaf length on geometric mean of average plot crown scorch and bole char heights. Fire severity shown is residual variation after accounting for season of fire effects. (b) Same as A, but *y*-axis shows residuals after accounting for proportion of pines in each plot, no significant relationship. (c) FE plots: effect of mean leaf length on total litter and duff consumed. (d) Same as C, but *y*-axis shows residuals after accounting for effect of proportion of pines.

Table 2. Summary of fit statistics for the two models classes tested for each data set. Model A represents the best-fit model, omitting a direct path between leaf length and fire severity; model B includes this path. The comparison statistics indicate the significance of the improvement in model B over A. Degrees of freedom (d.f.) differ among data sets because different non-significant paths were dropped when building the best-fit model A. The CBI-MC row shows results when Composite Burn Index (CBI) data were restricted to mixed conifer elevations (1800–2400 m). The CBI-Rx row shows results obtained for a subset of the CBI data set including only prescribed fire plots and omitting wild fires

Data set	Model A			Model B			Comparison with model A	
	χ^2	d.f.	P	χ^2	d.f.	P	$\Delta\chi^2$	P
Fire and Fire Surrogate (FFS)	9.81	5	0.102	4.56	4	0.335	5.25	0.022
Fire Effects (FE)	7.30	6	0.293	3.36	5	0.64	3.94	0.047
Composite Burn Index (CBI)	5.40	4	0.249	3.12	3	0.375	2.28	0.131
CBI-MC	4.78	4	0.311	4.51	3	0.211	0.03	0.862
CBI-Rx	15.19	4	0.004	3.14	3	0.371	11.95	0.0005

severity, geometric mean of crown scorch and bole char heights. The model including the direct leaf length to fire severity path was a significant improvement over the model lacking this path ($\Delta\chi^2 = 5.25$, $P = 0.022$, Table 2). In the best-fit model, slope and insolation positively influenced leaf length and this in turn influenced fire severity (Fig. 4a). Additionally, there was a significant direct effect of plot slope on fire severity: steeper slopes resulted in higher bole char and crown scorch regardless of species composition. In this model, the effect of insolation on fire severity was entirely explained by the effect that insolation has on species composition and leaf length. In this data set, elevation did not influence species composition nor fire severity. For this data set, the alternative model in which percentage contribution of *Pinus* to basal area replaced mean leaf length behaved similarly, but was a slightly poorer fit to the data ($\chi^2 = 5.6$, $P = 0.22$). In either case, there was evidence of a causal link between species composition and fire severity.

Similarly, for the FE data set, there was support for Model B over Model A ($\Delta\chi^2 = 3.94$, $P = 0.047$, Table 2, Fig. 4b). Slope and insolation had positive effects on leaf length and elevation had a negative effect. In turn, leaf length positively influenced litter consumption. In this data set, elevation was the only environmental variable directly influencing fire severity: higher elevation sites had reduced litter consumption regardless of species composition. An alternative model using proportion pines instead of leaf length had very poor model fit ($\chi^2 = 16.4$, $P = 0.038$). In this data set, leaf length again played a causal role in increasing fire severity.

For the largest-scale data set, the CBI plots, eliminating non-significant paths led to dropping slope entirely from the model, and there was no indication of a causal link between any variable and fire severity. Further investigation showed that in this data set the several measures of fire severity (the combined score ('ptmean'), the satellite dNBR values and the percentage plot burned) all co-varied, but there was only very weak linkage between any of the environmental predictors and these severity measures (model not shown). Across this wide range of plots, there were no environmental nor community composition indicators of fire severity. Similarly, when these data were limited to plots at mixed conifer elevations (1800–2400 m), there was very little structure to the data and no indication of an effect of leaf size (Table 2).

When this data set was restricted to only prescribed fires, a weak pattern emerged similar to that seen in the other data sets with a significant improvement in model fit when a direct path between leaf length and fire severity was included (Fig. 4c). The model fit was poorer than that obtained in the other data sets and showed that elevation negatively influenced leaf length and this reduced leaf length reduced fire severity. Restricted to only mixed conifer forest, the data produced no good-fit model (this set of plots was similar to the prescribed fire set but included a few wildfire plots and excluded low-elevation *P. ponderosa* forest).

Discussion

Despite the scientific interest in possible feedback effects of flammability traits on community assembly and trait evolution (Mutch 1970; Bond & Midgley 1995; Schwilk & Ackerly 2001; Schwilk & Kerr 2002; Schwilk 2003; Bond & Keeley 2005), examples specifically attributing fire behaviour differences to community composition, let alone to trait values, are rare. Most previous studies have focused on broad-scale differences across vegetation boundaries (e.g. Bowman & Wilson 1988; Geldenhuys 1994). Previous landscape-level analyses have often implicated species composition as a possible influence on fire regime (Beaty & Taylor 2001; Bekker & Taylor 2001; Blarquez, Bremond & Carcaillet 2010; Odion, Moritz & DellaSala 2010), but the effect that smaller-scale variation in community composition may have on local fire behaviour has been less studied. In their work describing heterogeneity in fire severity in the FFS study, Knapp & Keeley (2006) reported greater fuel consumption in areas dominated by pines, but the relative importance of abiotic site conditions and species composition was not tested. In our analysis, support for a leaf-length effect on fire severity is relatively strong in the data sets restricted to mixed conifer forest (FFS and FE data). This pattern is striking in that the leaf-length effect was significant even among the FFS plots, which differ from one another primarily in relative species abundances rather than representing broad shifts in community type. These results suggest that subtle shifts in species abundance can influence fire behaviour.

Variation in community composition within a forest type influences litter flammability. This effect is captured well by
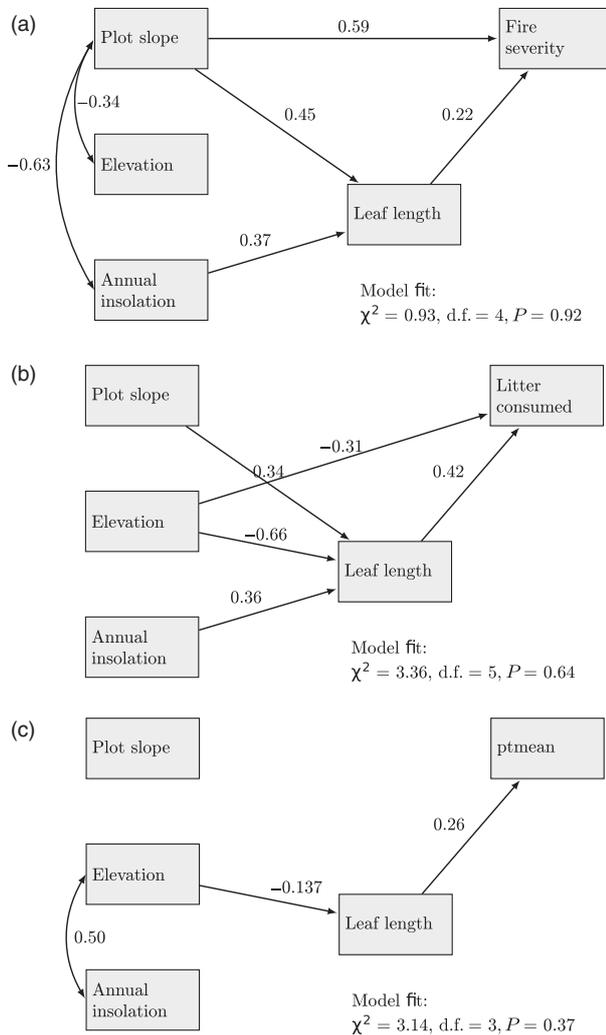
Fig. 4. Best-fitting observed variable models for each data set. Standardized path coefficients are shown for each significant path. (a) Fire and Fire Surrogate data (FFS), (b) Fire Effects data (FE), and (c) Composite Burn Index (CBI) data restricted to prescribed fires.

community mean leaf length and the causal influence of leaf length is consistent with experimental studies (Scarff & Westoby 2006). In our data, however, we can not make absolute conclusions regarding the causal role of leaf length, because this community variable is confounded with proportional contribution of *Pinus* to the community. It is possible that other conserved characteristics of *Pinus* may contribute to increased flammability (e.g. terpene concentrations in dry leaf litter). Several lines of evidence, however, suggest that leaf length is the best explanation for the pattern: (i) past experimental tests of leaf size and flammability (Scarff & Westoby 2006) and the relationship between leaf length and litter bulk density (our leaf-length data, van Wagtendonk, Benedict & Sydoriak 1998a), (ii) the fact that structural equation models using proportion pines rather than leaf length were poorer fitting and (iii) the fact that leaf length was a good predictor of litter consumption even after accounting for the effect of proportion pines in the FE data (Fig 3). In the FFS data, models including leaf length behaved marginally better than models using pro-

portion pines, but in a simple linear model, proportion pines explained the community composition effect (Fig. 3). The FFS plots represent a fairly homogeneous forest relative to the wider range of species composition found in the FE data. Only two pines, *P. jeffreyi* and *P. ponderosa*, are common and have very similar leaf lengths. The shorter-leaved *P. lambertiana* is relatively rare in the FFS plots and it not surprising, therefore, that it is more difficult to distinguish the effect of pines from the effect of leaf length in these data than it is in the FE data where *P. lambertiana* is more common.

Although the structural equation modelling approach is a powerful tool to detect causal relationships, any conclusions regarding causality are necessarily tentative and based on accumulating evidence. In our case, if some unmeasured variable jointly influences community composition and also fire severity, then our conclusions regarding the direct effect of leaf length on fire severity may not hold. We have confidence that our environmental variables are those important to predicting species occurrence on this landscape (Stephenson 1988) and our exploration of additional environmental variables (relative slope position and several subsets of insolation measures; results not shown) found that these correlated poorly with community composition.

None of the landscape variables nor community leaf length predict fire severity in the largest-scale CBI data. There are several possible explanations for this. First, the CBI data provide the coarsest measures of species composition among the three data sets. Second, fuel structure varies across this wide elevation range: at higher elevations, these plots include sub-alpine forest in which litter may play a small role in fire behaviour, while at lower elevations, these data include *P. ponderosa* forest in which both needle litter and herbaceous fuels drive fire. Third, these data include plots in wild fire, and burning conditions in wild fires are more variable than during prescribed fires; under such variable conditions the effect of leaf size on litter characteristics may be overwhelmed by exogenous variation in fire intensity.

When these CBI data were restricted to prescribed fires, the leaf-length effect became significant, but the correlation structure remained weak overall, which we suspect is due to the very coarse data available in this data set. This selection also biases the data towards lower-elevation plots and the leaf size effect may only be important in these more productive forests where leaf material is a significant portion of the surface fuels. When we restricted the analysis to only a subset of elevations that match the elevations found in the FFS and FE data, however, no pattern emerges (Table 2). Our conclusions regarding this data set are tentative – given the coarser nature of the data, we cannot conclusively point to the inclusion of high- and low-elevation forest types as the explanation for the lack of a leaf-length effect in the CBI data.

For the models examined, we have assumed that leaf litter flammability should respond to community composition as the mean leaf size of the litter, but this relationship has yet to be mechanistically examined for these species. Recent lab-based burning experiments demonstrate the potential relationship between leaf size and flammability measures in

Australian woodlands (Scarff & Westoby 2006) and in some North American *Quercus* species (Kane, Varner & Hiers 2008), but how such results scale to multi-species mixtures is still unknown. It is possible that such scaling is non-additive and further research in this area is needed. There is some evidence for non-additive effects of community composition on litter decomposition rates (reviewed in Hattenschwiler, Tiunov & Scheu 2005), and it seems possible that combinations of species that differ in flammability components may create similar non-additive effects. Leaf length acts as a good predictor of bulk density and litter bed ventilation, but the actual distribution of litter particle sizes will depend upon decomposition rate as well as initial size. Within a community, leaf decomposition rate is highly correlated with leaf economic spectrum traits: species with high leaf nitrogen and low leaf mass per area have high decomposition rates (Cornwell *et al.* 2008). In our system we find a single leaf trait (length) that can predict local fire severity, but among a larger group of species, it is likely that litter flammability is best predicted by at least a second dimension of green leaf trait variation associated with decomposition rate. Because leaf mass per area predicts leaf decomposition rate within a community, combining leaf mass per area and leaf size as dual predictors of fire severity may be a fruitful approach.

Although we measured only leaf length, other studies have used leaf area as a predictor of litter packing (Scarff & Westoby 2006). Leaf area is linked hydraulically and biomechanically with other aspects of plant canopy architecture: leaf area is correlated with twig size and inversely related to branching ramification (Corner 1949; White 1983; Ackerly & Donoghue 1998; Westoby & Wright 2003). Furthermore, small leaves and twigs tend to have dense wood, a trait correlated with greater resistance to drought-induced embolism of conducting vessels (Hacke *et al.* 2001). These trait associations suggest that selection for particular hydraulic and architectural traits may indirectly influence litter flammability. The functional significance of leaf area has traditionally been approached from the perspective of leaf boundary layer which influences gas exchange and energy balance. How the twig size–leaf size spectrum is linked to other patterns of trait variation is poorly understood – for example, leaf area is not part of the tightly linked suite of leaf economic traits (Wright *et al.* 2004). If litter flammability has fitness consequences, then flammability may be part of the explanation for leaf size variation.

We are learning a great deal about how plant community composition can shift in response to both large-scale aspects of fire regime and local-scale heterogeneity in fire severity in these forests (e.g. Schwilk *et al.* 2006; Knapp *et al.* 2007). This current work demonstrates the potential for these changes to, in turn, influence fire regime. In the mixed conifer forests of the Sierra Nevada, a primary management objective is to re-introduce fire. However, the shift to short-l species following fire exclusion has reduced fire severities. This positive feedback effect in which fire exclusion results in lower surface fire severity (although the increase in ladder fuels can increase crown fire risk) may be reversed with fire restoration as longer-leaved, shade-intolerant *Pinus* species again dominate forest landscapes. It is possible that as managers reduce overall fuel load and modify species composition, they will shift the system towards vegetation that is more flammable. This changed community may burn with greater severity, given a similar fuel load, in subsequent fires. Long-term fire severities may not be reduced to the degree originally predicted based only on the reduction in fuel loads. Increases in flammability will also likely result in greater rates of fire spread and affect other fire behaviour characteristics. The extent of these changes will reflect the relative species composition that exists following fire, which in many cases will continue to change over time with continued burning. This increased flammability may in part be an explanation for some of the high-frequency pre-EuroAmerican fire return intervals estimated from the fire scar record in areas where contemporary fires will not carry at such short intervals. Fire managers may need to compensate for these changes by adjusting burn prescriptions, by burning in a cooler season, or by reducing time between burns.

Understanding this feedback loop between species composition and fire regime will require a greater understanding of how litter traits influence fire. A more mechanistic perspective is especially important as managers attempt to predict fire behaviour in plant communities that are changing. As modified fire regimes and climate change shift the species composition of communities, we will increasingly be faced with novel species combinations. Ongoing climate change is predicted to result in no-analogue climates and, consequently, in novel plant assemblages as well (Williams, Jackson & Kutzbach 2007). Palaeoecological evidence suggests that climate, community composition and fire regime have been inextricably linked (Williams & Jackson 2007; Gill *et al.* 2009; Higuera *et al.* 2009). Human changes to fire regime and ongoing climate change will continue to modify community composition at multiple spatial scales. Work investigating how plant traits influence flammability has the potential to improve current predictions of fire behaviour and help to explain past fire regimes.

Acknowledgements

References

Ackerly, D.D. & Donoghue, M.J. (1998) Leaf size, sapling allometry, and Corner's Rules: phylogeny and correlated trait evolution in maples (*Acer*). *American Naturalist*, **152**, 767–791.

Barbour, M., Kelley, E., Maloney, P., Rizzo, D., Royce, E. & Fites-Kaufmann, J. (2002) Present and past old-growth forests of the Lake Tahoe Basin, Sierra Nevada, US. *Journal of Vegetation Science*, **13**, 461–472.

Beaty, R.M. & Taylor, A.H. (2001) Spatial and temporal variation of fire regimes in a mixed conifer forest landscape, Southern Cascades, California, USA. *Journal of Biogeography*, **28**, 955–966.

Behm, A., Duryea, M., Long, A. & Zipperer, W. (2004) Flammability of native understory species in pine flatwood and hardwood hammock ecosystems

and implications for the wildland-urban interface. *International Journal of Wildland Fire*, **13**, 355–365.

Bekker, M. & Taylor, A. (2001) Gradient analysis of fire regimes in montane forests of the southern Cascade range; Thousand Lakes Wilderness; California; USA. *Plant Ecology*, **155**, 15–28.

Blarquez, O., Bremond, L. & Carcaillet, C. (2010) Holocene fires and a herb-dominated understorey track wetter climates in subalpine forests. *Journal of Ecology*, **18**, 1358–1368.

Bond, W.J. & Keeley, J.E. (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution*, **20**, 387–394.

Bond, W.J. & Midgley, J.J. (1995) Kill thy neighbour: an individualistic argument for the evolution of flammability. *Oikos*, **73**, 79–85.

Bond, W.J., Woodward, F.I. & Midgley, G.F. (2005) The global distribution of ecosystems in a world without fire. *New Phytologist*, **165**, 525–538.

Bowman, D.M.J.S. & Wilson, B.A. (1988) Fuel characteristics of coastal monsoon forests, Northern Territory, Australia. *Journal of Biogeography*, **15**, 807–817.

Bradstock, R. & Cohn, J. (2002) Fire regimes and biodiversity in semi-arid mallee ecosystems. In *Flammable Australia: The Fire Regimes and Biodiversity of a Continent* (eds R. Bradstock, J. Williams & A. Gill). pp. 238–258, Cambridge University Press, Cambridge, UK.

Brown, J., Oberheu, R. & Johnston, C. (1982) Handbook for inventorying surface fuels and biomass in the interior west. Technical Report General Technical Report INT-129, USDA Forest Service, Fort Collins.

Bylesjö, M., Segura, V., Soolanayakanahally, R., Rae, A., Trygg, J., Gustafsson, P., Jansson, S. & Street, N. (2008) LAMINA: a tool for rapid quantification of leaf size and shape parameters. *BMC Plant Biology*, **8**: http://www.biomedcentral.com/1471-2229/8/82.

Corner, E. (1949) The durian theory, or the origin of the modern tree. *Annals of Botany*, **13**, 368–414.

Cornwell, W., Cornelissen, J., Amatangelo, K., Dorrepaal, E., Eviner, V., Godoy, O. *et al.* (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*, **11**, 1065–1071.

Dearden, F.M., Dehlin, H., Wardle, D.A. & Nilsson, M.C. (2006) Changes in the ratio of twig to foliage in litterfall with species composition, and consequences for decomposition across a long term chronosequence. *Oikos*, **115**, 453–462.

Díaz, S. & Cabido, M. (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution*, **16**, 646–655.

Dimitrakopoulos, A. (2001) A statistical classification of mediterranean species based on their flammability components. *International Journal of Wildland Fire*, **10**, 113–118.

Fox, J. (2006) Structural equation modeling with the sem package in R. *Structural Equation Modeling*, **13**, 465–486.

Ganteaume, A., Jappiot, M., Lampin-Maillet, C., Curt, T. & Borgniet, L. (2009a) Fuel characterization and effects of wildfire on limestone soils in southeastern France. *Forest Ecology and Management*, **258S**, S15–S23.

Ganteaume, A., Lampin-Maillet, C., Guijarro, M., Hernando, C., Jappiot, M., Fonturbel, T., Perez-Gorostiaga, P. & Vega, J. (2009b) Spot fires: fuel bed flammability and capability of firebrands to ignite fuel beds. *International Journal of Wildland Fire*, **18**, 951–969.

Garnier, E., Cortez, J., Billes, G., Navas, M.L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C. & Toussaint, J.P. (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, **85**, 2630–2637.

Geldenhuys, C.J. (1994) Bergwind fires and the location pattern of forest patches in the southern Cape landscape, South Africa. *Journal of Biogeography*, **21**, 49–62.

Gill, J., Williams, J., Jackson, S., Lininger, K. & Robinson, G. (2009) Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. *Science*, **326**, 1100.

Grace, J.B. (2006) *Structural Equation Modeling and Natural Systems*. Cambridge University Press, Cambridge, UK.

Grime, J. (1979) *Plant Strategies and Vegetation Processes*. John Wiley & Sons, Chichester, UK.

Grime, J. (2001) *Plant Strategies, Vegetation Processes and Ecosystem Properties*, 2nd edn. John Wiley & Sons, Chichester, UK.

Hacke, U.G., Sperry, J.S., Pockman, W.T., Davis, S.D. & McCulloch, K.A. (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia*, **126**, 457–461.

Hattenschwiler, S., Tiunov, A.V. & Scheu, S. (2005) Biodiversity and litter decomposition interrestrial ecosystems. *Annual Review of Ecology Evolution and Systematics*, **36**, 191–218.

Higuera, P., Brubaker, L., Anderson, P., Hu, F. & Brown, T. (2009) Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. *Ecological Monographs*, **79**, 201–219.

Kane, J., Varner, J.M. & Hiers, J. (2008) The burning characteristics of southeastern oaks: Discriminating fire facilitators from fire impeders. *Forest Ecology and Management*, **256**, 2039–2045.

Kauffman, J.B., Cummings, D.L. & Ward, D.E. (1994) Relationships of fire, biomass and nutrient dynamics along a vegetation gradient in the Brazilian cerrado. *Journal of Ecology*, **82**, 519–531.

Keeley, J. (2009) Fire intensity, fire severity and burn severity: a brief review and suggested usage. *International Journal of Wildland Fire*, **18**, 116–126.

Kellman, M. (1984) Synergistic relationships between fire and low soil fertility in neotropical savannas: a hypothesis. *Biotropica*, **16**, 158–160.

Key, C. & Benson, N. (2006) Landscape assessment (la): Sampling and analysis methods. In *FIREMON: Fire Effects Monitoring and Inventory System* (ed. D. Lutes), RMRS-GTR-164-CD, pp. LA 1–55. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Knapp, E. & Keeley, J. (2006) Heterogeneity in fire severity within early and late season prescribed burns in a mixed conifer forest. *International Journal of Wildland Fire*, **15**, 37–45.

Knapp, E., Schwilk, D., Kane, J. & Keeley, J. (2007) Role of burning season on initial understory vegetation response to prescribed fire in a mixed conifer forest. *Canadian Journal of Forest Research*, **37**, 11–22.

Lavorel, S. & Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the holy grail. *Functional Ecology*, **16**, 545–556.

Lavorel, S., McIntyre, S., Landsberg, J. & Forbes, T.D.A. (1997) Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends in Ecology & Evolution*, **12**, 474–478.

van Mantgem, P. & Schwilk, D. (2009) Negligible influence of spatial autocorrelation in the assessment of fire effects in a mixed conifer forest. *Fire Ecology*, **5**, 116–125.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, **21**, 178–185.

Mutch, R.W. (1970) Wildland fires and ecosystems – a hypothesis. *Ecology*, **51**, 1046–1051.

Odion, D., Moritz, M. & DellaSala, D. (2010) Alternative community states maintained by fire in the Klamath Mountains, USA. *Journal of Ecology*, **98**, 96–105.

Parsons, D.J. & DeBennedetti, S.H. (1979) Impact of fire suppression on a mixed-conifer forest. *Forest Ecology and Management*, **2**, 21–33.

Philpot, C. (1977) Vegetative features as determinants of fire frequency and intensity. *In Proceedings of the Symposium on the Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems* (eds H. Mooney & C. Conrad), pp. 12–16. USDA Forest Service Technical Report WO-3, Washington, DC.

Plucinski, M. & Anderson, W. (2008) Laboratory determination of factors influencing successful point ignition in the litter layer of shrubland vegetation. *International Journal of Wildland Fire*, **17**, 628–637.

Scarff, F.R. & Westoby, M. (2006) Leaf litter flammability in some semi-arid Australian woodlands. *Functional Ecology*, **20**, 745–752.

Schwilk, D. (2003) Flammability is a niche construction trait: Canopy architecture affects fire intensity. *American Naturalist*, **162**, 725–733.

Schwilk, D.W. & Ackerly, D.D. (2001) Flammability and serotiny as strategies: correlated evolution in pines. *Oikos*, **94**, 326–236.

Schwilk, D.W. & Kerr, B. (2002) Genetic niche-hiking: an alternative explanation for the evolution of flammability. *Oikos*, **99**, 431–442.

Schwilk, D.W., Knapp, E., Ferrenberg, S., Keeley, J. & Caprio, A. (2006) Tree mortality from fire and bark beetles following early and late season prescribed fires in a Sierra Nevada mixed conifer forest. *Forest Ecology and Management*, **232**, 36–45.

Southwood, T. (1988) Tactics, strategies and templets. *Oikos*, **52**, 3–18.

Stephenson, N. (1988) Climatic control of vegetation distribution: the role of the water-balance with examples from North America and Sequoia National Park, California. PhD Thesis, Cornell University, Ithaca, NY.

Sundarapandian, S.M. & Swamy, P.S. (1999) Litter production and leaf-litter decomposition of selected tree species in tropical forests at Kodayar in the Western Ghats, India. *Forest Ecology and Management*, **123**, 231–244.

Swetnam, T. & Baisan, C. (2003) Tree-ring reconstructions of fire and climate history in the Sierra Nevada and Southwestern United States. *In Fire and climatic change in temperate ecosystems of the western Americas* (eds T. Veblen, W. Baker, G. Montenegro & T. Swetnam), pp. 158–195, Springer, New York, NY, USA.

USDI National Park Service (2003) *Fire Monitoring Handbook*, Fire Management Program Center, National Interagency Fire Center, Boise, ID, USA.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the concept of trait be functional!. *Oikos*, **116**, 882–892.

van Wagtendonk, J.W., Benedict, J.M. & Sydoriak, W.M. (1996) Physical properties of woody fuel particles of Sierra Nevada conifers. *International Journal of Wildland Fire*, **6**, 117–123.

van Wagtendonk, J.W., Benedict, J.M. & Sydoriak, W.M. (1998a) Fuel bed characteristics of Sierra Nevada conifers. *Western Journal of Applied Forestry*, **13**, 73–84.

van Wagtendonk, J.W., Sydoriak, W.M. & Benedict, J.M. (1998b) Heat content variation of Sierra Nevada conifers. *International Journal of Wildland Fire*, **8**, 147–158.

Westoby, M. & Wright, I. (2003) The leaf size - twig size spectrum and its relationship to other important spectra of variation among species. *Oecologia*, **135**, 621–628.

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002) Plant ecological strategies: Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, **33**, 125–159.

White, P. (1983) Corner's rules in eastern deciduous trees: allometry and its implications for the adaptive architecture of trees. *Bulletin of the Torrey Botanical Club*, **110**, 203–212.

van Wilgen, B.W., Higgins, K. & Bellstedt, D. (1990) The role of vegetation structure and fuel chemistry in excluding fire from forest patches in the fire-prone fynbos shrublands of South Africa. *Journal of Ecology*, **78**, 210–222.

Williams, J. & Jackson, S. (2007) Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, **5**, 475–482.

Williams, J., Jackson, S. & Kutzbach, J. (2007) Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences*, **104**, 5738.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F. et al. (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.

Supporting Information

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Table S1. Leaf and branchlet lengths.

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