

Shifts in community-level traits and functional diversity in a mixed conifer forest: a legacy of land-use change

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Summary

1. Historical reference conditions have long been used to guide the restoration of degraded ecosystems. However, a rapidly changing climate and altered disturbance regimes are calling into question the usefulness of this approach. As a consequence, restoration goals are increasingly focused on creating communities that are resilient to novel environmental stressors and emphasis is being placed on defining functional targets through the use of plant traits. While changes in forest structure and composition have received much attention, long-term changes in stand-level functional traits are not well understood.

2. We used dendrochronology to reconstruct historical forest structure and composition in 1880, the year immediately following the disruption of the natural fire regime in a mixed conifer forest in Arizona, USA. We analysed the differences in pre-settlement and contemporary forest composition, structure and community-weighted mean (CWM) traits, and functional diversity metrics (Rao's Q and functional richness) for four plant functional traits: leaf nitrogen content (leaf N), specific leaf area (SLA), wood density and bark thickness.

3. We observed significant shifts in forest composition, structure, CWM traits and functional diversity from 1880 to 2011. These changes reflect a reduction in fire and drought tolerance, driven largely by increases in the relative importance of *Abies concolor* and *Pinus strobiformis*. Compositional changes were associated with declines in CWM leaf N, SLA, wood density and bark thickness. We found lower multitrait functional diversity (Rao's Q) in contemporary forests driven primarily by leaf N; however, bark thickness variation was greater in contemporary forests than in 1880.

4. *Synthesis and applications.* Compositional shifts towards reduced average bark thickness and wood density in contemporary forests driven by land-use change have likely reduced forest resilience to both fire and drought. Managers can manipulate forest structure and species composition to achieve functional objectives by increasing stand-level bark thickness to promote fire tolerance and increasing stand-level wood density to promote drought tolerance. Forecasts for extended fire seasons along with declining precipitation are projected for many ecosystems around the planet. A focus on restoring optimal functional trait combinations may be as important as managing ecosystem structure for restoring resilient ecosystems.

Key-words: bark thickness, community structure, frequent fires, functional diversity, functional traits, leaf economics, leaf nitrogen, mixed conifer forest, specific leaf area, wood density

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Introduction

Synergistic effects of climate and wildfire constrain the distribution and abundance of tree species around the world (Bond, Woodward & Midgley 2005). As weather patterns trend towards warmer and drier conditions, the size and severity of forest wildfires will intensify in many regions (Westerling *et al.* 2006), and ecosystems are likely to experience novel combinations of environmental conditions and disturbances (Hobbs, Higgs & Harris 2009). Anticipating ecological responses to these processes is relevant to restoration practitioners attempting to meet multiple management objectives. Recent advances in trait-based restoration ecology offer promise in addressing these problems (Laughlin 2014; Ostertag *et al.* 2015).

Mixed conifer forests of the western United States are complex in terms of structure and disturbance regimes (Romme, Floyd & Hanna 2009). Based on the variation in abiotic and biotic conditions, two major mixed conifer subtypes are widely recognized: a 'warm/dry' type and a 'cool/moist' type. This study focuses on the former of the two forest types. Warm/dry forests were historically dominated by fire-tolerant *Pinus ponderosa* Lawson & C. Lawson and *Pseudotsuga menziesii* (Mirb.) Franco but also included *Quercus gambelii* Nutt., *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr., *Pinus strobiformis* Engelm. and *Populus tremuloides* Michx. (Romme, Floyd & Hanna 2009). There is strong evidence that composition was regulated by frequent, low-intensity surface fires that burned at mean return intervals ranging 2–30 years. (Grissino-Mayer *et al.* 2004; Huffman, Zegler & Fulé 2015).

Over the last century, intensive land uses including unregulated livestock grazing, selective timber harvesting and active fire suppression have resulted in significant shifts in forest composition and structure in warm/dry mixed conifer forests (Fulé, Korb & Wu 2009). A major consequence of this has been large increases in tree densities and a shift in dominance towards more shade- and fire-intolerant species (Huffman, Zegler & Fulé 2015). In turn, wildfires in these forests have become increasingly more severe (Westerling *et al.* 2006). There is a concerted effort to mitigate this risk through landscape-scale restoration efforts (Schultz, Jedd & Beam 2012). Restoration treatments are based largely on applying the concept of reference conditions and the natural range of variability, defining targets based on historical forest structure and composition (Roccaforte *et al.* 2015).

Although recent changes in contemporary forest structure and composition have received much attention, functional trait responses related to these changes are not fully understood. Studies have shown that shifts in structure and composition have been primarily due to decreasing relative importance of fire-tolerant *P. ponderosa* and *P. menziesii* (Korb, Fulé & Wu 2013; Huffman, Zegler & Fulé 2015). A significant decline of the historically dominant species can restrict the ability of practitioners to define species-specific targets using historical composition

and structure. Additionally, as climate change progresses, forest ecosystems in many regions are expected to experience conditions outside of their natural range of variability, increasing the probability of widespread mortality and large-scale disturbance events (Williams *et al.* 2010). As a consequence, defining restoration targets based on historical conditions might become less relevant. One alternative is for restoration practitioners to focus on restoring resilient ecosystems by targeting functional attributes better adapted to anticipated future environmental conditions.

A trait-based approach offers a complementary alternative that focuses restoration efforts on meeting functional targets (Ostertag *et al.* 2015). Functional targets can be defined based on historical reference conditions or future desired conditions under anticipated environmental changes (Laughlin *et al.* 2016). Defining functional targets based on historical conditions would provide a useful complement when the loss of historically dominant species makes it difficult to restore past forest composition and structure. In this case, species abundance distributions can be targeted that meet historical wood density, bark thickness or fire tolerance indices. Alternatively, in systems that lack reference information, practitioners may want to increase fire tolerance by targeting species abundance distributions that increase stand-level bark thickness (Pausas 2015), or may want to increase wood density to enhance drought tolerance (Laughlin *et al.* 2011). Applying a trait-based framework requires an understanding of how traits confer fitness under different environmental conditions and management practices (Garnier & Navas 2012).

Recent work in comparative ecology has identified two independent axes of plant specialization. The leaf economics spectrum (LES) describes a gradient from species with short-lived leaves that allow for the acquisition and processing of carbon, nutrients and water more rapidly than those with longer-lived leaves that reduce carbon and nutrient turnover (Reich 2014). Species with leaf traits that allow for the quick acquisition of resources tend to dominate in early successional, higher resource environments compared to species that use a more conservative resource use strategy (Reich 2014). Leaf traits associated with the LES such as specific leaf area (SLA, ratio of leaf area to dry mass) and nutrient concentrations have also been shown to influence litter flammability (Grootemaat *et al.* 2015). This has important implications in semi-arid environments where litter accumulation is high and fine surface fuels are the primary source of surface fire spread (Bradstock & Cohn 2002). The wood economics spectrum (WES) describes a gradient from species with dense wood with low tissue moisture content to species with lower wood density and higher moisture content (Baraloto *et al.* 2010). Higher density wood confers greater resistance to drought-induced cavitation (Hacke *et al.* 2001) and may also play a role in fire tolerance by allowing species to compartmentalize damage and reduce the risk of mortality (Romero & Bolker 2008; Brando *et al.* 2012). Bark thickness has been shown to align with the WES (Baraloto *et al.* 2010) and represents

a key adaptation related to fire resistance (Jackson, Adams & Jackson 1999).

Our objective was to assess century-long changes in overstorey forest composition, structure and functional diversity in a warm/dry mixed conifer forest where the historical surface fire regime was interrupted ca 1880 and where subsequent selective harvesting occurred in the mid-1900s (e.g. Huffman, Zegler & Fulé 2015). This land-use history is common in mixed conifer forests of the western United States. Community-weighted mean (CWM) traits are useful for assessing the changes in the dominant trait values within a community and can be related to successional shifts in plant strategies (Lohbeck *et al.* 2013). Functional diversity reflects the variation in trait values present within a community (Mason & de Bello 2013) and can be useful for understanding how environmental filtering influences community assembly (Enquist *et al.* 2015). We analysed four traits that together represent the LES and WES and reflect important characteristics of species adapted to semi-arid, frequent-fire ecosystems. We asked the following questions: (i) 'How have forest composition and structure changed since fire exclusion in 1880?'; (ii) 'How have community-level SLA, leaf N, wood density, bark thickness and functional diversity changed since fire exclusion in 1880?'; and (iii) 'Do the long-term changes reflect a shift in fire tolerance on the landscape?'

Materials and methods

STUDY SYSTEM

We conducted our study within a 1135-ha warm/dry mixed conifer ecosystem on the Black Mesa Ranger District of the Apache-Sitgreaves National Forest in northern Arizona (34°22'38.57"N & 111°0'15.18"W). Elevation on the site ranges from 2313 to 2405 m with an average annual precipitation of 695 mm and average temperature of 5.5 °C (Laing *et al.* 1987; Fig. 1). Overstorey community composition was composed of the following tree species: *P. ponderosa*, *P. menziesii*, *Q. gambelii* Nutt., *Pinus strobiformis* Engelm., *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr., *Populus tremuloides* Michx., *Acer grandidentatum* Nutt. and *Robinia neomexicana* A. Gray (Table 1). Topography of the site is characterized by gently sloping terrain bisected by small, steep drainages with infrequent rock outcroppings present.

Huffman, Zegler & Fulé (2015) found that the last major fire at the site occurred in 1879; only one scar recording a fire date after this time was identified across 133 wood samples (1023 cross-dated fire scars). Similar fire regime disruptions have been widely documented in western frequent-fire forests and linked to intensive, unregulated livestock grazing associated with industrialization as well as active fire suppression (Covington & Moore 1994). Recent livestock grazing has not occurred at the site. In addition, large cut stumps of *P. ponderosa* and *P. menziesii* trees at the site evidenced extensive selective timber harvesting that took place across the Mogollon Rim in the mid-1900s (Huffman, Zegler & Fulé 2015; Rodman *et al.* 2016).

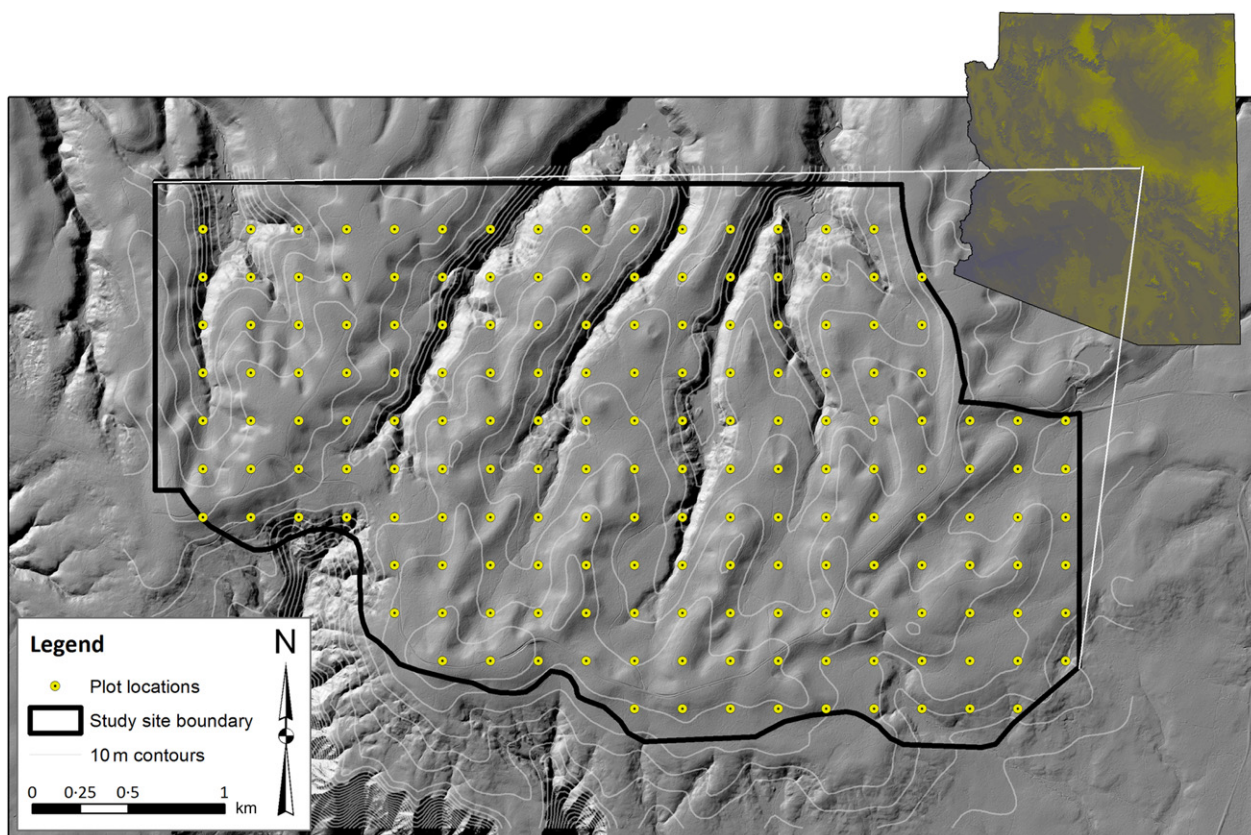


Fig. 1. Study site and plot (0.04-ha, $n = 146$) location map for the Black Mesa mixed conifer study site on the Apache-Sitgreaves National Forest near Heber, Arizona.

Table 1. Names, codes and fire tolerance weights (w_{FT}) for tree species occurring at the Black Mesa mixed conifer study site. Species are sorted from most fire-tolerant to fire-intolerant based on the information from Reynolds *et al.* (2013)

Species	Common name	Code	w_{FT}
<i>Pinus ponderosa</i> P. & C. Lawson	Ponderosa pine	PIPO	12
<i>Pseudotsuga menziesii</i> (Mirb.) Franco	Douglas-fir	PSME	10
<i>Quercus gambelii</i> Nutt.	Gambel oak	QUGA	8
<i>Pinus strobiformis</i> Engelm.	South-western white pine	PIST	6
<i>Populus tremuloides</i> Michx.	Quaking aspen	POTR	4
<i>Abies concolor</i> (Gordon & Glendinning) Hoopes.	White fir	ABCO	2
<i>Robinia neomexicana</i> A. Gray	New Mexico locust	RONE	1
<i>Abies lasiocarpa</i> (Hooker) Nuttall	Subalpine fir	ABLA	1
<i>Acer grandidentatum</i> Nutt.	Bigtooth maple	ACGR	1

FOREST STRUCTURE

Current overstorey composition and structure were determined using 146 permanent 0.04-ha plots, arrayed on a 250-m systematic grid originating from a randomly selected starting point within the project area. Grid point locations were generated using a geographic information system (ARCGIS 9.3; Environmental Systems Research Institute, Redlands, CA, USA) and overlaid on a site map. Points were used as centres of circular (11.28-m-radius) sample plots on which species and condition for all trees present, both living and dead, were recorded. Diameter at breast height (dbh, measured at 1.37 m height on stem) was recorded for live trees, and diameter at stump height (dsh, measured at 40 cm above root collar) was recorded for dead trees. Increment cores were collected at dsh from all live trees presumed to be ≥ 130 years old and a random sample (10%) of younger trees. For conifers, increment cores were collected from all live trees ≥ 37.5 cm dbh; we collected cores from all aspen trees ≥ 20 cm dbh, and from all oak, maple and locust ≥ 17 cm dbh, following the methods described in Fulé, Covington & Moore (1997).

In the absence of fire, wood decomposition in the south-west is extremely slow and evidence of remnant tree structures (i.e. stumps, snags, logs) from the late 1800s is still readily apparent (Fulé, Covington & Moore 1997; Sánchez Meador & Moore 2010). This remnant evidence in combination with contemporary forest structure can be used to develop reliable forest reconstructions (Huffman *et al.* 2001). To quantify the forest composition and structure prior to fire exclusion, we used techniques of dendrochronology (Stokes & Smiley 1996) and the process outlined by Bakker (2005) and Fulé, Covington & Moore (1997) to reconstruct historical tree basal area, density and composition on each plot. In brief, we used live and dead (stumps, snags, logs, etc.) tree morphological characteristics combined with increment cores to determine tree age, with species-specific basal area increment, tree allometry (e.g. bark thickness equations from Laughlin *et al.* 2011) and snag and log decomposition (Rogers *et al.* 1984) equations to determine the historical status (live or dead) and size of all trees sampled prior to fire exclusion. These methods have been validated and are widely used in *P. ponderosa* and mixed conifer

forests in the south-west. Comparisons of reconstructed stand conditions with actual historical data indicate that these methods are reliable within $\pm 10\%$ (Huffman *et al.* 2001; Moore *et al.* 2004) and robust to assumptions (Fulé, Covington & Moore 1997; Sánchez Meador & Moore 2010). We chose to reconstruct forest conditions in the year 1880, which represented conditions at the time of disruption of the natural fire regime at our site (Huffman, Ziegler & Fulé 2015). Reconstructing forest structure to an earlier date would not be appropriate given that the frequent fires during this time would have likely consumed much of the downed woody material.

FUNCTIONAL STRUCTURE

We assessed the changes in functional structure using four functional traits: leaf nitrogen content (leaf N), specific leaf area (SLA), wood density and bark thickness. Trait values were obtained for each species using standardized methods as described in Appendix S1 (Supporting Information).

Two important metrics were calculated to describe the changes in overstorey functional structure. First, we calculated a community-weighted mean (CWM) trait value for each trait in both the reconstructed historical forest and the contemporary forest. A CWM trait value was calculated as:

$$\sum_{i=1}^s t_{ij} p_{ik}, \quad \text{eqn 1}$$

where t_{ij} is the average value of trait j for species i and p_{ik} is the relative abundance of species i in plot k . In this study, we used importance values (IV)s as our measure of abundance and calculated the proportions of relative abundance based on IVs for each species at the plot level. Importance values represent a measure of dominance of species in a given community by combining tree density and basal area. Plot-level species importance values (IV: *sensu* Curtis & McIntosh 1951) were calculated as:

$$IV_i = \left(\left(\frac{BA_i}{BA_{k\text{total}}} \right) \cdot 100 \right) + \left(\left(\frac{D_i}{D_{k\text{total}}} \right) \cdot 100 \right), \quad \text{eqn 2}$$

where BA_i is the basal area ($\text{m}^2 \text{ha}^{-1}$) and D_i the density (trees ha^{-1}) of species i , respectively, and $BA_{k\text{total}}$ and $D_{k\text{total}}$ are the total basal area and tree density in plot k . Therefore, a CWM trait value (i.e. eqn 1) calculated using relative importance (i.e. p_{ik} eqn 1) can be interpreted as the CWM value expressed by an individual of average importance.

To examine the influence of species dominance on plot- and landscape-scale fire tolerance, a plot-level fire tolerance index was calculated as:

$$FTI = \sum_i^n (IV \cdot w_{FT}), \quad \text{eqn 3}$$

where IV is the importance value for species i calculated using eqn 2, w_{FT} are the species-specific fire tolerance weights from Table 1. Fire tolerance weights range in value from 12, signifying high species fire tolerance, to 1, signifying low species tolerance, and were determined from the information provided in Reynolds *et al.* (2013). The resulting plot-level FTI values represent a measure of relative fire tolerance, ranging from ≤ 1000 (highly fire-intolerant plot-level importance values) to ≥ 2000 (highly fire-tolerant). Lastly, we examined the changes or heterogeneity in fire

tolerance variability, both temporally and spatially, by quantifying and comparing the observed change in plot-level FTI value frequency and autocorrelation (Moran 1950) for the landscape in 1880 and 2011.

Next, we quantified the functional trait diversity for each trait using two indices: functional richness and Rao's quadratic entropy (hereafter referred to as functional diversity; Botta-Dukát 2005). Functional richness is calculated as the minimum convex hull that includes all species in T-dimensional space. Functional richness describes the volume of trait space filled by the community and has been shown to perform well in communities with low richness (Mouchet *et al.* 2010). Calculations of multitrait functional richness require the number of species in a community to be greater than the number of traits. Because this was not strictly the case (i.e. many plots had fewer than five species), we chose to calculate single-trait functional richness indices. For a single trait, functional richness indices represent a measure of the range of trait values within a community. Functional diversity (i.e. Rao's quadratic entropy) is a measure of functional divergence and takes into account both the range of functional space and the similarity between species weighted by their relative abundance. As such, diversity characterizes the degree to which the species are distributed towards the most extreme values within the community (Mouchet *et al.* 2010). Because diversity is not limited by species richness, we calculated both multitrait and single-trait diversity indices. Both diversity and functional

richness were calculated using the `FD` package in `R` (Laliberté, Legendre & Shipley 2014).

DATA ANALYSIS

First, we examined the differences between the reconstructed 1880 (i.e. pre-settlement) and contemporary 2011 forest composition and structural attributes using permutational multivariate analysis of variance (PERMANOVA; Anderson 2001). This method is appropriate for ecological data because it avoids strict assumptions of normality. A dissimilarity matrix can be obtained using distance measures appropriate for multivariate (i.e. Bray–Curtis distance) data. Differences in basal area, trees ha^{-1} and importance values were examined with time as a fixed effect. Next, differences in community-weighted mean (CWM) trait values, functional diversity (i.e. Rao's quadratic entropy) and functional richness before (1880) and after (2011) fire exclusion were tested using a paired Wilcoxon signed-rank test. All analyses were conducted at $\alpha = 0.05$ in `R` ver. 3.1.3 (R Core Development Team 2015). Lastly, changes in fire tolerance were explored by computing a single-step transition matrix (Asmussen 2003) for species dominance of FTI on all plots as reconstructed following fire exclusion. That is, the transition matrix is the matrix consisting of the transition probabilities from state x to state y , r_{xy} , based on estimates derived from changes in species dominance in FTI for each plot over the 132-year study period (from 1880 to 2011). Because the sum total probability of transitioning from an initial state i to some state j must be 1, this matrix is a right stochastic matrix, so that the $\sum_j r_{xy} = 1$.

Table 2. PERMANOVA results for compositional differences in basal area, tree density and importance values between pre-settlement (1880) and contemporary (2011) data

Source	d.f.	MS	F	P
Basal area ($\text{m}^2 \text{ha}^{-1}$)				
Time	1	11.79	46.93	<0.001
Residuals	290	0.25	0.86	
Total	291	1.00		
Tree density (trees ha^{-1})				
Time	1	18.25	88.98	<0.001
Residuals	290	0.21	0.77	
Total	291	1.00		
Importance value				
Time	1	7.59	42.23	<0.001
Residuals	290	0.18	0.87	
Total	291	1.00		

Results

OVERSTOREY COMPOSITION AND STRUCTURE

We found significant differences between pre-settlement (1880) and contemporary (2011) forest composition in terms of basal area, tree density and species importance values (Table 2). Pre-settlement basal area was dominated by *P. ponderosa* and *P. menziesii* with average contributions of 39% and 28%, respectively. *Abies concolor* and *Q. gambelii* each contributed 11%. *Pinus strobiformis*, *P. tremuloides* and *A. grandidentatum* represented minor components, averaging <1% of the total basal area (Table 3).

Table 3. Pre-settlement (1880) and contemporary (2011) forest structural attributes. Standard errors are presented in parentheses. Species codes are given in Table 1 and sorted by fire tolerance

Species	Basal area ($\text{m}^2 \text{ha}^{-1}$)		Density (tree ha^{-1})		Importance value	
	1880	2011	1880	2011	1880	2011
PIPO	3.57 (0.38)	8.22 (0.86)	45.2 (3.3)	172 (40.0)	87.9 (5.60)	43.4 (4.14)
PSME	2.61 (0.58)	7.83 (0.59)	28.9 (3.1)	186 (16.3)	39.2 (4.03)	45.8 (2.93)
QUGA	1.01 (0.20)	2.44 (0.35)	30.9 (3.9)	52.9 (5.2)	29.2 (3.18)	16.6 (1.81)
PIST	0.51 (0.19)	4.51 (0.62)	5.1 (1.4)	142 (14.4)	8.34 (2.27)	29.2 (2.44)
POTR	0.42 (0.13)	0.29 (0.12)	9.6 (2.5)	2.9 (1.1)	10.5 (2.50)	0.97 (0.38)
ABCO	1.04 (0.23)	7.99 (0.67)	19.0 (2.3)	261 (19.3)	23.7 (3.13)	60.1 (3.51)
RONE	–	0.01 (0.01)	–	0.5 (0.3)	–	0.18 (0.13)
ABLA	–	0.01 (0.01)	–	0.1 (0.1)	–	0.06 (0.06)
ACGR	0.01 (0.01)	0.34 (0.12)	2.1 (1.1)	26.7 (11.5)	1.11 (0.51)	3.74 (1.22)
Totals	9.18	31.62	140.4	844.13	200	200

Pre-settlement size distribution was heavily right skewed (Fig. 2a). *Pinus ponderosa* dominated the 15-cm to 35-cm and ≥ 75 -cm size classes, *P. menziesii* and *Q. gambelii* were consistently represented across all size classes, and *A. concolor* was present in most size classes, including 0.17 tree ha⁻¹ in the 95-cm size class (Fig. 2a). By 2011, overall basal area had increased from 9.18 to 31.63 m² ha⁻¹. *Pinus ponderosa* basal area had more than doubled yet its overall contribution declined to 26% (Fig. 2b). *Pseudotsuga menziesii* also increased in absolute terms, yet its average contribution to basal area declined 13%. *Abies concolor* basal area increased to an average of 23% of total basal area, whereas the basal area contribution of *Q. gambelii* decreased from pre-settlement to make up 1% of total BA. *Pinus strobiformis* represented an average of 14% of the total basal area in 2011, with marked increases in tree densities under the 25-cm size class.

Reconstructed pre-settlement tree density averaged 140 trees ha⁻¹ (Table 3). *Pinus ponderosa* accounted for the majority (32%) at 45 trees ha⁻¹, followed by *Q. gambelii*

(22%) at 31 trees ha⁻¹, *P. menziesii* (29 trees ha⁻¹) and *A. concolor* (19 trees ha⁻¹). Mean tree density increased to 844 tree ha⁻¹ by 2011. *Abies concolor* was the dominant species numerically and contributed an average of 31% to total tree density, followed by *P. menziesii* (22%) and *P. ponderosa* (20%). *Quercus gambelii*'s contribution declined to 6%. *Acer grandidentatum* increased in both absolute and relative terms yet contributes <5% to total tree density.

Prior to fire exclusion, *P. ponderosa* was the most important species in the pre-settlement 1880 forest, followed by *P. menziesii*, *Q. gambelii*, *A. concolor* and *P. tremuloides*, respectively (Table 4). By 2011, *A. concolor* was the most important species in contemporary forests, followed by *P. menziesii*, *P. ponderosa*, *P. strobiformis* and *Q. gambelii*. The majority of *P. ponderosa*-dominated FTIs (fire tolerance index) remained dominated by fire-tolerant species (i.e. *P. ponderosa* and *P. menziesii*) with a third transitioning to *A. concolor* and the remainder becoming *P. strobiformis*. Contemporary FTIs were clearly domi-

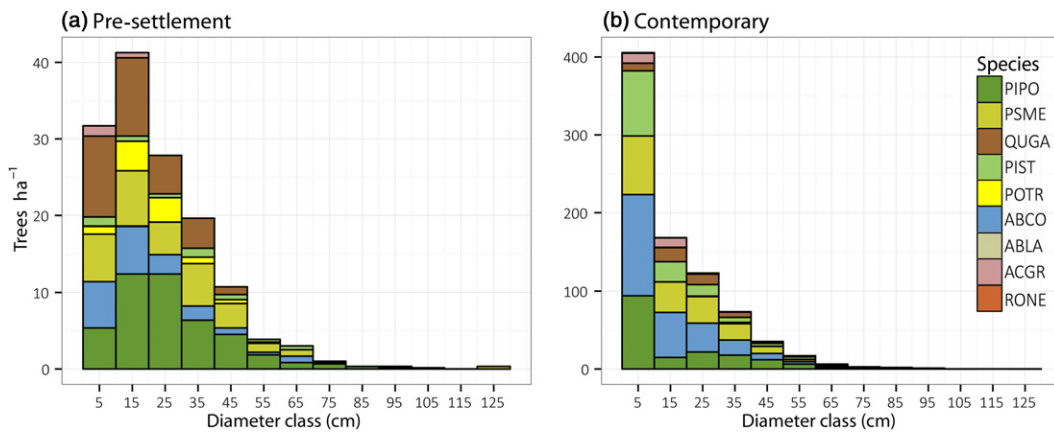


Fig. 2. Species-specific diameter distributions in (a) pre-settlement (1880) and (b) contemporary (2011) time periods. The list of species is sorted by fire tolerance from highest to lowest. Note the order of magnitude difference between y-axes in panels a and b.

Table 4. Single-step (132-years) transition matrix for species dominance of importance index on all plots (0.04-ha, n = 146) observed at Black Mesa mixed conifer study site between pre-settlement (1880) and contemporary (2011) conditions

		Contemporary									
Species		PIPO	PSME	QUGA	PIST	POTR	ABCO	RONE	ABLA	ACGR	Total
Pre-settlement	PIPO	0.34	0.23	0.01	0.10	–	0.30	–	–	–	0.53
	PSME	0.16	0.36	–	0.08	–	0.40	–	–	–	0.17
	QUGA	0.08	0.23	0.23	–	–	0.46	–	–	–	0.09
	PIST	–	0.33	–	0.50	–	0.17	–	–	–	0.04
	POTR	–	0.30	–	0.10	–	0.60	–	–	–	0.07
	ABCO	0.13	0.20	–	0.07	–	0.60	–	–	–	0.10
	RONE	–	–	–	–	–	–	–	–	–	0.00
	ABLA	–	–	–	–	–	–	–	–	–	0.00
	ACGR	–	–	–	–	–	–	–	–	–	0.00
	Total	0.23	0.26	0.03	0.10	0.00	0.38	0.00	0.00	0.01	1.00

Values indicate species dominance (sorted by fire tolerance) shifts (from 1880 to 2011) in fire tolerance index and thus observed changes in species importance. Larger transition probabilities are indicated by progressively darker tones of grey. Total values for each column represent species dominance transitions from pre-settlement to contemporary conditions expressed as the proportion of plots transitioning.

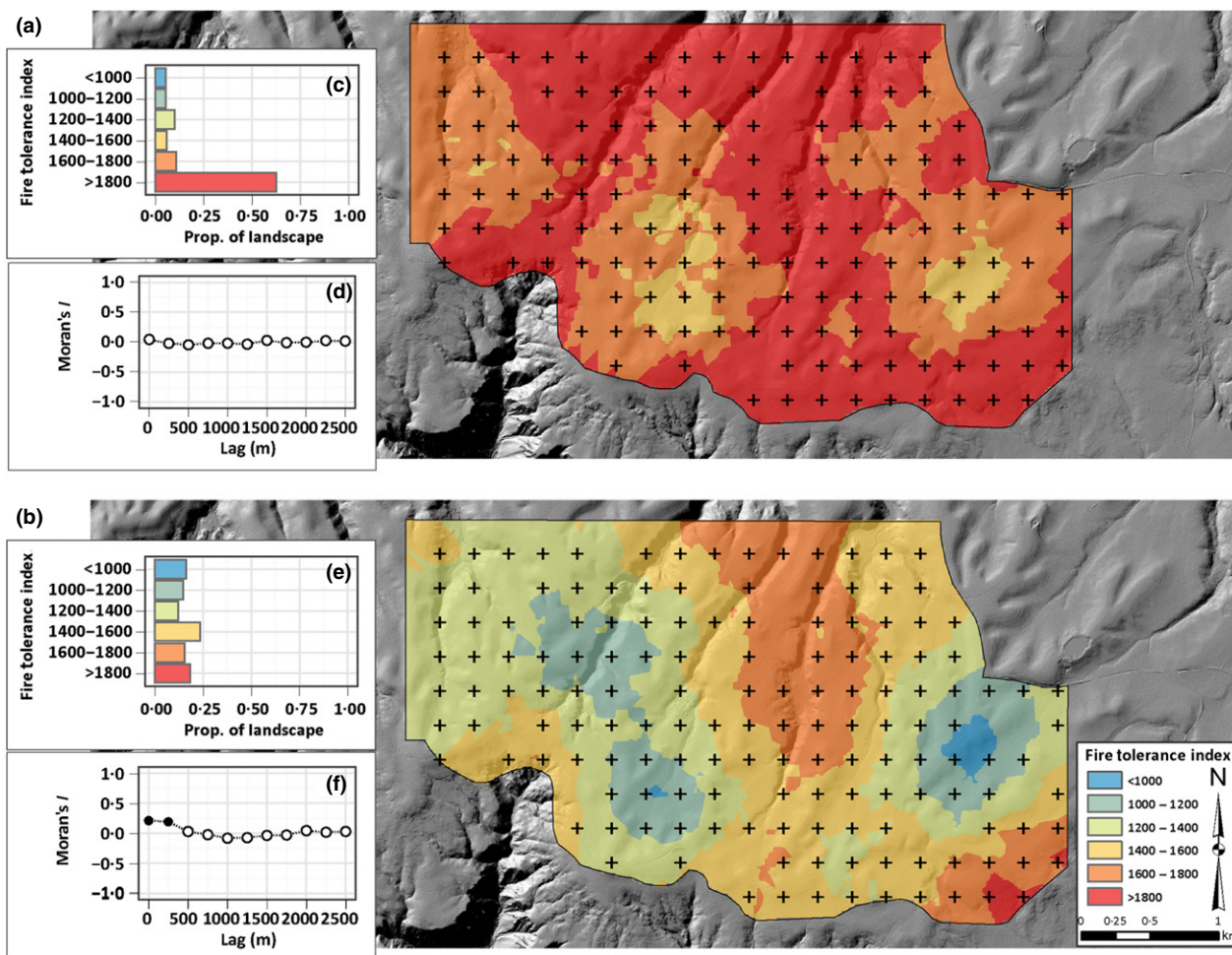


Fig. 3. Inverse distance-weighted interpolation of fire tolerance index in 1880 (a) and 2011 (b) and corresponding plot-level landscape proportions ($n = 146$) and spatial autocorrelograms for six classes of fire tolerance index. For the latter, black circles indicate the significance in autocorrelation ($P < 0.001$) for the given lag.

nated by *A. concolor* (55 plots or 38% of the landscape), with the majority of these transitioning from either *P. ponderosa* (42%) or *P. menziesii* (18%). Lastly, the majority of the historically aspen-dominated plots (10 plots or 7% of the landscape) transitioned to have FTIs dominated by either *A. concolor* (60%) or *P. menziesii* (30%). While the landscape as a whole transitioned from largely fire tolerant to intolerant, areas of higher fire tolerance persisted and overall heterogeneity in fire tolerance increased from 1880 to 2011 (Fig. 3). Spatially, the historical FTI values for the landscapes were found to be independent, with contemporary conditions exhibiting statistically significant spatial autocorrelation at distances at or below 250 m (Fig. 3d,e).

FUNCTIONAL TRAITS

We found significant directional shifts in all four CWM traits between 1880 and 2011 (Table 5). Bivariate trait densities (Fig. 4) revealed that contemporary forests converged on lower SLA, leaf N, wood density and bark thickness. Since the late 1800s, community-weighted mean

SLA declined by 7%, leaf N by 10%, wood density by 4% and bark thickness by 11% (Table 5).

Shifts in trait means over time were accompanied by shifts in trait variances as well. Contemporary forest conditions exhibited significantly lower multitrait functional diversity, indicating that the volume of trait space was more fully occupied in pre-settlement forests. Lower multitrait diversity was driven by a significant decline in the individual diversity of leaf N. Functional richness of leaf N also declined, indicating a narrower range of values in the contemporary forest compared with the forest of 1880. In contrast, both functional richness and diversity of bark thickness increased in the contemporary forest. No difference in individual trait diversity of SLA or wood density was detected; however, functional richness of both traits increased from 1880 to 2011 (Table 5).

Discussion

This study advances our understanding of reference conditions and natural range of variability by quantifying historical forests in terms of plant functional traits. The

Table 5. Functional attributes (mean \pm SD) in pre-settlement (1880) and contemporary (2011) time periods

Functional attributes	Pre-settlement	Contemporary	Wilcoxon signed-rank test	
			V	P
CWM traits				
SLA	6.23 \pm 0.18	5.74 \pm 0.18	6811	0.001
Leaf N (%)	1.52 \pm 0.33	1.37 \pm 0.15	8482	<0.0001
Wood density	0.46 \pm 0.04	0.44 \pm 0.03	8911	<0.0001
Bark thickness	15.0 \pm 3.20	13.4 \pm 2.40	8717	<0.0001
Functional richness				
SLA	0.66 \pm 0.05	0.87 \pm 0.06	2090	<0.0001
Leaf N (%)	1.21 \pm 0.87	0.93 \pm 0.58	7301	<0.0001
Wood density	1.15 \pm 0.89	1.50 \pm 0.77	2837	<0.0001
Bark thickness	1.31 \pm 0.77	1.95 \pm 0.63	1523	<0.0001
Diversity (Rao's Q)				
Multitrait	1.13 \pm 0.07	0.94 \pm 0.06	6664	0.004
SLA	0.11 \pm 0.02	0.15 \pm 0.03	6172	0.05
Leaf N (%)	0.35 \pm 0.33	0.11 \pm 0.11	9122	<0.0001
Wood density	0.32 \pm 0.33	0.28 \pm 0.27	5642	0.4006
Bark thickness	0.35 \pm 0.28	0.39 \pm 0.23	4150	0.0329

contemporary mixed conifer forest was significantly different in overstorey composition, structure, fire tolerance, CWM traits and functional diversity than the 1880 forest. Forests in 1880 appeared relatively open, largely fire tolerant and dominated by shade-intolerant, fire-tolerant species (Reynolds *et al.* 2013). Multitrait diversity was high as were CWM SLA, leaf N, wood density and bark thickness. Over the last 132 years, significant increases in tree densities and basal area have altered the distribution of species relative importance resulting in lower CWM trait values and diversity. Together, this has led to increases in both heterogeneity in fire tolerance at the landscape scale (up to 2500 \times 2500 m or 650 ha, distance across study site) and homogeneity at small scales (\leq below 250 \times 250 m or 6.25 ha, distance between plots). These changes likely resulted from the combined impacts of fire suppression and selective harvesting practices that began in the late 19th century (Huffman, Zegler & Fulé 2015).

Greater CWM SLA and leaf N in 1880 reflected greater dominance of *Q. gambelii* and *P. tremuloides*. These species resprout rapidly after fire, reflecting a key adaptation for persistence in fire-prone ecosystems (Pausas & Bradstock 2007). This corresponds to the findings of Huffman, Zegler & Fulé (2015), who noted large increases in tree establishment following fire regime disruption and suggested that historical surface fires likely maintained more open forest conditions. Greater light availability would have allowed *Q. gambelii* and *P. tremuloides* to pre-emptively acquire resources and out-compete slower-growing, shade-tolerant species. Leaves with higher SLA and nutrient concentrations (e.g. leaf N) have faster ignition rates but lower flame and smouldering durations (Murray,

Hardstaff & Phillips 2013; Grootemaat *et al.* 2015). Although herbaceous understorey species, which contribute fine fuels needed for frequent surface fires, exhibit these traits to a greater degree than woody species (Reich, Walters & Ellsworth 1997), our findings suggest that these functional adaptations also extend to the overstorey community. Selective harvesting of *P. ponderosa* and *P. menziesii* in the mid-1900s (Huffman, Zegler & Fulé 2015) likely allowed for an increase in establishment of fire-intolerant species and a greater range of SLA values. We also found a lower range of leaf N values along with a reduction in leaf N diversity, which indicated that the community became functionally more homogeneous in terms of leaf N.

Higher CWM wood density in 1880 forests corresponded to a greater importance of *P. ponderosa*, *P. menziesii* and *Q. gambelii*. Wood density is associated with hydraulic properties and drought tolerance (Chave *et al.* 2009). Our results suggest that the overstorey community may have been more tolerant to drought historically. In addition, wood density has been shown to influence wound closure rates, and species with denser woody could have a competitive advantage in isolating decay from surface fire wounds and thereby reducing mortality (Romero & Bolker 2008). Shifts in functional richness and diversity can be attributed to both fire exclusion and selective harvesting. These factors would have promoted the recruitment and establishment of additional species, leading to a greater range of wood density values and functional richness in contemporary forests. However, our results showed lower diversity and a more even distribution of trait values, indicating a community dominated by species similar in average wood density. Thus, historically fire was likely a strong environmental filter, which selected for higher mean wood density within a narrower range of values. Under these conditions, there was a greater relative abundance of species with unique trait values, namely *P. ponderosa*, *P. menziesii* and *Q. gambelii*.

Bark thickness was also thicker historically than in contemporary forests at the site. Lower CWM bark thickness in 2011 was driven primarily by lower relative importance of *P. ponderosa* (bark thickness mean = 19.9 mm) and increases in *P. strobiformis* (bark thickness mean = 7.6 mm). Bark thickness confers resistance to surface fire (Lawes *et al.* 2011). Our findings further indicate that fire played an integral role in determining the functional and taxonomic composition of forests at the study site. Increases in functional richness of bark thickness suggest that historically frequent surface fires restricted the viable range of trait values across these communities. In addition, a lower diversity of bark thickness in 1880 indicates that the forest was dominated by a few species with similar bark thickness.

The importance values used in our analysis accounted for relative species abundance in terms of both tree density and basal area. This is important in mixed species stands in which species differ in important life-history

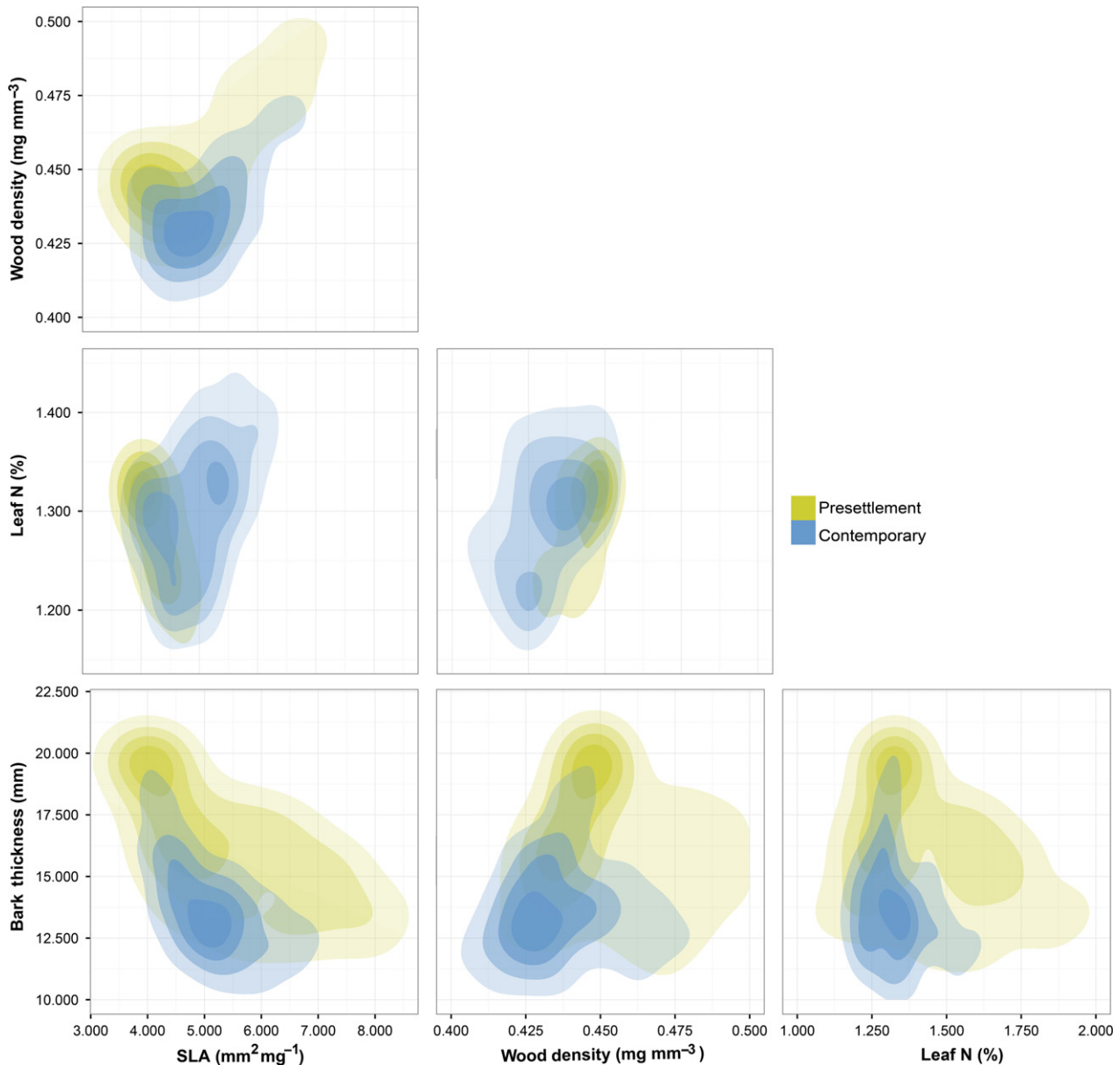


Fig. 4. Bivariate trait densities for wood density, leaf nitrogen (leaf N), specific leaf area (SLA) and bark thickness in pre-settlement (1880) and contemporary (2011) time periods. Different colour shades represent the density (in terms of quintiles) of co-occurring CWM trait values.

characteristics such as regeneration and growth. For example, within our community, *Q. gambelii* regenerates primarily through re-sprouting and as a result can be found at higher densities for a given area than *P. ponderosa*. In contrast, *P. ponderosa* is a larger species and will obtain a greater basal area at a given density compared to *Q. gambelii*. Analysis using a single metric, such as relative basal area (i.e. $BA_i/BA_{k\text{total}}$, eqn 2), yields qualitatively similar results to those using an importance index; however, there are differences that highlight the need to account for relative density (i.e. $D_i/D_{k\text{total}}$, eqn 2) as well (see Table S1). For example, when relative basal area is used to calculate CWM traits, SLA does not differ between time periods. In this case, no change in CWM SLA reflects a greater contribution, in terms of relative

abundance, of larger growing species in both time periods. Furthermore, pre-settlement CWM SLA and leaf N are lower when using only basal area because the contribution, in terms of relative abundance, of species such as *Q. gambelii* and *P. tremuloides*, is not accounted for adequately. Using basal area alone does not account for important life-history differences between species and may bias results towards larger species.

Our approach assumes that the temporal variation in intraspecific mean trait values was negligible. Historical climate and disturbance regimes experienced by individuals could have resulted in different average trait values than those expressed by individuals in contemporary forests. While the direction of change may be similar across species, trait plasticity may differ substantially between

species which could influence the rate at which trait values change (Enquist *et al.* 2015).

CONCLUSION AND MANAGEMENT IMPLICATIONS

Current conditions in temperate mixed conifer forests put them at increased susceptibility to high-severity fires and drought as a result of significant increases in tree densities and a shift in dominance towards more fire- and drought-intolerant species (Fulé, Korb & Wu 2009; Huffman, Zegler & Fulé 2015). These compositional and structural changes were associated with declines in CWM leaf N, SLA, wood density and bark thickness, and coincide with an overall decline in functional diversity.

Strategies for restoring ecological resilience and sustainability are a top priority for natural resource managers (Suding 2011), and a focus on plant traits may be useful to achieve this goal (Ostertag *et al.* 2015). This is due in part to recent advances in trait-based models that provide a mechanism for translating functional targets into distributions of species abundance (Laughlin 2014). Defining appropriate functional targets is fundamental to this approach. This study integrated historical changes in composition with shifts in community-level functional traits of a mixed conifer forest in western North America, but historical reference information is not always available. Functional traits are being applied in the restoration of multiple ecosystems throughout the planet (Ostertag *et al.* 2015; Cole *et al.* 2016), by basing restoration treatments on eco-physiological principles to achieve functional outcomes.

Eco-physiological adaptations to fire and drought provide a robust framework for restoring ecosystems under global change. Fire and drought are globally important disturbances that are projected to increase as a result of longer fire weather seasons in many ecosystems around the world (Jolly *et al.* 2015). Manipulating forest structure and composition to increase wood density and bark thickness could be a first step in restoring forests that are more resilient to increased fires and drought. Implementing this new framework will be challenging and require innovative approaches. A high priority for future research is to test the success and efficacy of restoring ecosystem resilience when management objectives are focused on functional traits.

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Data accessibility

Functional trait and plot-level overstorey data: Northern Arizona University Cline Library's Open Knowledge repository (<http://openknowledge.nau.edu/2933/>). These data are currently embargoed until 1 August 2017 due to its use in a separate manuscript.

References

- Anderson, M.J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, **26**, 32–46.
- Asmussen, S.R. (2003) Markov chains. *Applied probability and queues. Stochastic Modelling and Applied Probability*, **51**, 3–38.
- Bakker, J.D. (2005) A new, proportional method for reconstructing historical tree diameters. *Canadian Journal of Forest Research*, **35**, 2515–2520.
- Baraloto, C., Paine, C.E.T., Poorter, L., Beuchene, J., Bonal, D., Domenach, A.-M. *et al.* (2010) Decoupled leaf and stem economics in rain forest trees. *Ecology Letters*, **13**, 1338–1347.
- 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.
- Botta-Dukát, Z. (2005) Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science*, **16**, 533–540.
- Bradstock, R. & Cohn, J. (2002) Fire regimes and biodiversity in semi-arid mallee ecosystems. *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.
- Brando, P.M., Nepstad, D.C., Balch, J.K., Bolker, B., Christman, M.C., Coe, M. & Putz, F. (2012) Fire-induced mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behavior. *Global Change Biology*, **18**, 630–641.
- Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**, 351–366.
- Cole, I.A., Prober, S.M., Lunt, I.D. & Koen, T.B. (2016) A plant traits approach to managing legacy species during restoration transitions in temperate eucalypt woodlands. *Restoration Ecology*, **24**, 354–363.
- Covington, W.W. & Moore, M.M. (1994) Southwestern ponderosa pine forest structure. Changes since Euro-American settlement. *Journal of Forestry*, **92**, 39–47.
- Curtis, J.T. & McIntosh, R.P. (1951) An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology*, **32**, 476–496.
- Enquist, B.J., Norberg, J., Bonser, S.P., Violle, C., Webb, C.T., Henderson, A., Sloat, L.L. & Savage, V.M. (2015) Scaling from traits to ecosystems: developing a general trait driver theory via integrating trait-based and metabolic scaling theories. *Advances in Ecological Research*, **52**, 249–318.
- Fulé, P.Z., Covington, W.W. & Moore, M.M. (1997) Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. *Ecological Applications*, **7**, 895–908.
- Fulé, P.Z., Korb, J.E. & Wu, R. (2009) Changes in forest structure of a mixed conifer forest, southwestern Colorado, USA. *Forest Ecology and Management*, **258**, 1200–1210.
- Garnier, E. & Navas, M.-L. (2012) A trait-based approach to comparative functional plant ecology: concepts, methods and applications for agroecology. *Agronomy for Sustainable Development*, **32**, 365–399.
- Grissino-Mayer, H.D., Romme, W.H., Floyd, M.L. & Hanna, D.D. (2004) Climatic and human influences on fire regimes of the southern San Juan mountains, Colorado, USA. *Ecology*, **85**, 1708–1724.
- Grootemaat, S., Wright, I.J., van Bodegom, P.M., Cornelissen, J.H. & Cornwell, W.K. (2015) Burn or rot: leaf traits explain why flammability and decomposability are decoupled across species. *Functional Ecology*, **29**, 1486–1497.
- Hacke, U.G., Sperry, J.S., Pockman, W.T., Davis, S.D. & McCulloh, K.A. (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia*, **126**, 457–461.
- Hobbs, R.J., Higgs, E. & Harris, J.A. (2009) Novel ecosystems: implications for conservation and restoration. *Trends in Ecology and Evolution*, **24**, 599–605.
- Huffman, D.W., Zegler, T.J. & Fulé, P.Z. (2015) Fire history of a mixed conifer forest on the Mogollon Rim, northern Arizona, USA. *International Journal of Wildland Fire*, **24**, 680–689.
- Huffman, D.W., Moore, M.M., Covington, W.W., Crouse, J.E. & Fulé, P.Z. (2001) Ponderosa pine forest reconstruction: comparisons with historical data. In: Vance, R.K., Edminster, C.B., Covington, W.W., Blake (comps.), J.A. (Eds.), *Ponderosa pine ecosystems restoration and conservation: steps toward stewardship*. U.S. Forest Service RMRS-P-22, Washington, DC, USA, pp. 3–8.
- Jackson, J.F., Adams, D.C. & Jackson, U.B. (1999) Allometry of constitutive defense: a model and a comparative test with tree bark and fire regime. *The American Naturalist*, **152**, 614–632.

- Jolly, W.M., Cochrane, M.A., Freeborn, P.H., Holden, Z.A., Brown, T.J., Williamson, G.J. & Bowman, D.M.J.S. (2015) Climate-induced variations in global wildfire danger from 1979 to 2013. *Nature Communications*, **6**, 7537.
- Korb, J.E., Fulé, P.Z. & Wu, R. (2013) Variability of warm-dry mixed conifer forests in southwestern Colorado, USA: implications for ecological restoration. *Forest Ecology and Management*, **304**, 182–191.
- Laing, L., Ambos, N., Subirge, T., McDonald, C., Nelson, C. & Robbie, W. (1987) *Terrestrial Ecosystems Survey of the Apache-Sitgreaves National Forests*. USDA Forest Service, Southwest Region, Albuquerque, NM, USA.
- Laliberté, E., Legendre, P. & Shipley, B. (2014) FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12.
- Laughlin, D.C. (2014) Applying trait-based models to achieve functional targets for theory-driven ecological restoration. *Ecology Letters*, **17**, 771–784.
- Laughlin, D.C., Fulé, P.Z., Huffman, D.W., Crouse, J. & Laliberté, E. (2011) Climatic constraints on trait-based forest assembly. *Journal of Ecology*, **99**, 1489–1499.
- Laughlin, D.C., Strahan, R.T., Huffman, D.W. & Sánchez Meador, A.J. (2016) Using trait-based ecology to restore resilient ecosystems: historical conditions and the future of montane forests in western North America. *Restoration Ecology*, doi:10.1111/rec.12342.
- Lawes, M.J., Adie, H., Russell-Smith, J., Murphy, B. & Midgely, J.J. (2011) How do small savanna trees avoid stem mortality by fire? The roles of stem diameter, height and bark thickness. *Ecosphere*, **2**, 1–13.
- Lohbeck, M., Poorter, L., Lebrija-Trejos, E., Martínez-Ramos, M., Meave, J.A., Paz, H. *et al.* (2013) Successional changes in functional composition contrast for dry and wet tropical forest. *Ecology*, **94**, 1211–1216.
- Mason, N.W.H. & de Bello, F. (2013) Functional diversity: a tool for answering challenging ecological questions. *Journal of Vegetation Science*, **24**, 777–780.
- Moore, M.M., Huffman, D.W., Fulé, F.Z., Covington, W.W. & Crouse, J.E. (2004) Comparison of historical and contemporary forest structure and composition on permanent plots in southwestern ponderosa pine forests. *Forest Science*, **50**, 162–176.
- Moran, P.A.P. (1950) Notes on continuous stochastic phenomena. *Biometrika*, **37**, 17–37.
- Mouchet, M.A., Villéger, S., Mason, N.W.H. & Moullot, D. (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, **24**, 867–876.
- Murray, B.R., Hardstaff, L.K. & Phillips, M.L. (2013) Differences in leaf flammability, leaf traits and flammability-trait relationships between native and exotic plant species of dry sclerophyll forest. *PLoS ONE*, **8**, e79205.
- Ostertag, R., Warman, L., Cordell, S. & Vitousek, P.M. (2015) Using plant functional traits to restore Hawaiian rainforest. *Journal of Applied Ecology*, **52**, 805–809.
- Pausas, J.G. (2015) Bark thickness and fire regime. *Functional Ecology*, **29**, 315–327.
- Pausas, J.G. & Bradstock, R.A. (2007) Fire persistence traits of plants along a productivity and disturbance gradients in Mediterranean shrublands of south-east Australia. *Global Ecology and Biogeography*, **16**, 330–340.
- R Core Team (2015) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Reich, P.B. (2014) The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. *Journal of Ecology*, **102**, 275–301.
- Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997) From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the United States of America*, **94**, 13730–13734.
- Reynolds, R.T., Sánchez Meador, A.J., Youtz, J.A., Nicolet, T., Matonis, M.S., Jackson, P.L., DeLorenzo, D.G. & Graves, A.D. (2013) Restoring composition and structure in Southwestern frequent-fire forests: A science-based framework for improving ecosystem resiliency. Gen. Tech. Rep. RMRS-GTR-310. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 76 p.
- Roccaforte, J.P., Huffman, D.W., Fulé, P.Z., Covington, W.W., Chancellor, W.W., Stoddard, M.T. & Crouse, J.E. (2015) Forest structure and fuels dynamics following ponderosa pine restoration treatments, White Mountains, Arizona, USA. *Forest Ecology and Management*, **337**, 174–185.
- Rodman, K.C., Sánchez Meador, A.J., Huffman, D.W. & Waring, K.M. (2016) Reference conditions and historical fine-scale spatial dynamics in a dry mixed-conifer forest, Arizona, USA. *Forest Science*, **62**, 15–136.
- Rogers, J.J., Prosser, J.M., Garrett, L.D. & Ryan, M.G. (1984) ECOSIM: a system for projecting multiresource outputs under alternative forest management regimes. USDA Forest Service, Administrative Report, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.
- Romero, C. & Bolker, B.M. (2008) Effects of stem anatomical and structural traits on responses to stem damage: an experimental study in the Bolivian Amazon. *Canadian Journal of Forestry*, **38**, 611–618.
- Romme, W.H., Floyd, M.L. & Hanna, D. (2009) *Historical Range of Variability and Current Landscape Condition Analysis: South Central Highlands Section, Southwestern Colorado and Northwestern New Mexico*. Colorado Forest Restoration Institute, Colorado State University, Fort Collins, CO, USA.
- Sánchez Meador, A.J. & Moore, M.M. (2010) Lessons from long-term studies of harvest methods in southwestern ponderosa pine-Gambel oak forests on the Fort Valley Experimental Forest, Arizona, U.S.A. *Forest Ecology and Management*, **260**, 193–206.
- Schultz, C.A., Jedd, T. & Beam, R.D. (2012) The collaborative forest landscape restoration program: a history and overview of the first projects. *Journal of Forestry*, **110**, 381–391.
- Stokes, M.A. & Smiley, T.L. (1996) *An Introduction to Tree-Ring Dating*. University of Chicago Press, Chicago, IL, USA.
- Suding, K.N. (2011) Toward an era of restoration in ecology: success, failures, and opportunities ahead. *Annual Review of Ecology, Evolution, and Systematics*, **42**, 465–487.
- Westerling, A.L., Hidalgo, H.G., Cayan, D.R. & Swetnam, T.W. (2006) Warming and earlier spring increase western US forest wildfire activity. *Science*, **313**, 940–943.
- Williams, A.P., Allen, C.D., Millar, C.I., Swetnam, T.W., Michaelsen, J., Still, C.J. & Leavitt, S.W. (2010) Forest responses to increasing aridity and warmth in the southwestern United States. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 21289–21294.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Functional trait measurements.

Table S1. Methodological details.