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RESEARCH PAPER

Spatially extensive reconstructions show variable-severity fire and heterogeneous structure in historical western United States dry forests

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ABSTRACT

Aim Wildfire is often considered more severe now than historically in dry forests of the western United States. Tree-ring reconstructions, which suggest that historical dry forests were park-like with large, old trees maintained by low-severity fires, are from small, scattered studies. To overcome this limitation, we developed spatially comprehensive reconstructions across 927,000 ha in four landscapes, using a new method based on land surveys from *c.* 1880.

Location Dry forests of the western United States.

Methods We reconstructed forest structure for four large dry-forest landscapes using forest descriptions and tree data from historical land surveys. Using multiple elements of historical forest structure from this study along with corroborating information from tree-ring studies, we were able to interpret past forest dynamics. Hypotheses concerning historical structure and dynamics were then tested.

Results These reconstructions show that dry forests were structurally variable, containing from 20 to over 1000 trees ha^{-1} and some dense understoreys of shrubs and small trees. Park-like stands of large trees maintained by low-severity fire predominated only in parts of the study landscapes. Only 3, 12, 40 and 62% of the four landscapes fit a low-severity fire model; 38–97% had evidence of *higher*-severity (mixed- and high-severity) fire. Some large modern wildfires (e.g. Rodeo-Chediski), perceived as catastrophic, had fire severity congruent with historical variability.

Main conclusions Spatially extensive reconstructions from the late 1800s show that these forests were structurally variable, including areas of dense forests and understorey trees and shrubs, and fires varied in severity, including 15–65% high-severity fire. A set of laws, policies and initiatives that aim to uniformly reduce fuels and fire severity is likely to move many of these forests outside their historical range of variability with adverse effects on biological diversity. Macroscale survey-based reconstructions and palaeoecological studies reveal that *higher*-severity fires were and are a part of the normal dynamics of dry forests.

Keywords
Fire regime, forest restoration, historical forest structure, GLO surveys, landscape reconstruction, ponderosa pine, spatial heterogeneity, variable-severity fire, western United States.

INTRODUCTION

Wildfire is thought to be increasing globally in response to warming temperatures and human-induced changes in fuels (Liu *et al.*, 2010) but interpreting these changes requires baseline information about historical fire regimes and vegetation, which may be limited or unresolved. For example, high-severity forest fire, where most canopy trees are killed, is often considered

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historically abnormal in dry forests of the western United States (e.g. Allen *et al.*, 2002). Tree-ring and fire-scar reconstructions, historical records and early photographs suggest dry forests had large, widely spaced, old ponderosa pines (*Pinus ponderosa* C. Lawson), or other fire-tolerant trees, with a grassy understorey and few shrubs or small trees, maintained by frequent, low-severity fires (Covington & Moore, 1994; Allen *et al.*, 2002). Fire severity is thought to have increased over the last 150 years because of fuel build-up (e.g. increased small, shade-tolerant trees) from fire exclusion, timber harvesting and livestock grazing (Covington & Moore, 1994). Reacting to large recent fires perceived as unnaturally severe, a set of policies and laws (e.g. Healthy Forests Restoration Act of 2003; Federal Land Assistance, Management and Enhancement Act of 2009) seeks to reduce high-severity fire in dry forests by thinning small trees and reintroducing fire at short intervals, in keeping with this low-severity fire model. These efforts are expensive and have some negative ecological impacts (Odion *et al.*, 2004; Hutto, 2008), and evidence to support them is spatially and temporally incomplete.

Historical information and reconstructions of forest structure and fire severity are typically available for few locations, which are often of limited spatial extent and uneven coverage (Morgan *et al.*, 2001); for example, they are common in Arizona (Abella & Denton, 2009) but rare in Oregon. Even with expanded tree-ring reconstructions at multiple locations (e.g. Abella & Denton, 2009), spatial coverage is incomplete and conflicting across the western United States. Available evidence supports the low-severity fire model at many locations (see Table S1 in supporting information). However, this model is rejected in some studies (Brown *et al.*, 1999; Ehle & Baker, 2003; Hessburg *et al.*, 2007), where an alternative variable-severity fire model (i.e. mixed-severity with evidence of both low- and high-severity fire) may apply. Furthermore, many studies and resource-management plans ignore the impacts of climatic variability on forest structure and fire severity, even though climate has been found to be a primary driver of fire regimes (Pierce *et al.*, 2004; Trouet *et al.*, 2006; Jenkins *et al.*, 2011). Here we address the matter of spatially incomplete coverage. We ask whether more spatially extensive data (i.e. > 100,000 ha) would reveal historical dry forests of the western USA to have had a relatively uniform low-density, park-like structure associated with low-severity fire or more variable structure and fire severity?

To address this question, we greatly expand available reconstructions of historical forest structure and fire severity using spatially extensive General Land Office (GLO) survey data (*c.* 1880) with new statistical techniques that together are nearly as accurate as tree-ring reconstructions (Williams & Baker, 2011). The GLO surveys, originally designed for land subdivision, constitute a systematic survey of vegetation that can be used to reconstruct forest structure over vast land areas (e.g. 138,000 km^2; Bollinger *et al.*, 2004). We analysed GLO-survey section-line descriptions and bearing-tree data to reconstruct forest structure and fire severity across four large western dry-forest landscapes: (1) Mogollon Plateau, AZ, (2) Black Mesa, AZ, (3) Front Range, CO, and (4) Blue Mountains, OR (Fig. 1). The

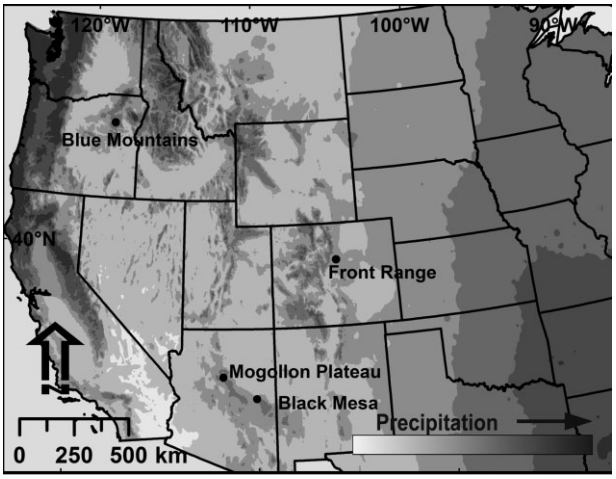

Figure 1 Location of study areas with background precipitation. Precipitation data provided by Daly & Taylor (2009).

GLO-survey data include descriptions of forest composition and structure along survey lines, and samples of trees, including species, size and distance from survey markers (Williams & Baker, 2010). Surveyors described *c.* 3.2 km of section lines and recorded data for eight trees per 2.6 km^2. Our analysis is based on a GIS dataset from survey notes including about 13,000 section-line descriptions for 20,700 km of survey lines over 1,680,000 ha and data for about 28,500 trees at 3600 section corners over 927,000 ha in the four landscapes.

We analysed these data to test three hypotheses, which reflect current understanding about historical dry-forest landscapes: H_1, forest structure and composition were relatively uniform and similar within and among regions, with low-density, park-like forests, containing few shrubs or shade-tolerant trees, across large landscapes; H_2, low-severity fire prevailed across all landscapes and high-severity fire was rare; H_3, rates of high-severity fire were low and have increased. The temporal resolution of survey-based reconstructions is limited to the decades before widespread Euro-American settlement, which is only part of the relevant era of historical variability (Keane *et al.*, 2009). However, if evidence from this period rejects the hypotheses, they can probably be rejected for the broader range of historical variability.

METHODS

Study landscapes

Dry forests in the western United States are broadly defined (Hann *et al.*, 1997), but generally include abundant ponderosa pine, with lesser amounts of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.), grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.), juniper (*Juniperus* L.), western larch (*Larix occidentalis* Nutt.) and lodgepole pine (*Pinus contorta* Douglas ex Louden). Ponderosa pine occurs from Mexico into southern Canada; its distribution is limited by soil moisture deficit at lower elevations

and short growing season at higher elevations (Hann *et al.*, 1997). These forests commonly occur near human settlements, and they are often exploited and in need of restoration (Baker *et al.*, 2007). We selected ponderosa pine/dry mixed-conifer forests using ReGAP maps, vegetation maps from LANDSAT satellite data with 30-m resolution (e.g., Lowry *et al.*, 2005). Reconstruction boundaries included townships with adequate surveys (see Williams & Baker, 2011) and little or no Euro-American land uses (e.g. logging) before the surveys.

Forest landscape reconstructions

Bearing-tree data from the GLO survey can be used with new statistical methods we have developed (Williams & Baker, 2011) to accurately reconstruct tree density, species composition and diameter-class distributions for trees > 10 cm diameter breast height (d.b.h.) in dry forests. Data from survey notes were input into ArcGIS (ESRI, Redlands, CA, USA) for analysis. Density reconstructions use the mean area occupied by a tree, estimated by the tree's Voronoi area (Delincé, 1986), which is calculated using the tree's diameter, crown radius and density of neighbouring trees (Williams & Baker, 2011). Composition and diameter-class distributions were reconstructed using the fraction of trees of each species and within 10-cm diameter bins.

Accurate estimation requires pooling of tree data across survey corners, to increase sample size, at different levels depending on the forest-structure parameter (Williams & Baker, 2011). Tree density was estimated for pools of six corners (518 ha), composition for nine corners (777 ha) and diameter-class distributions for 12 corners (1036 ha), based on accuracy trials. These trials showed that accuracy of density estimates varied from 14.4 to 23% compared with plot estimates, while composition was 89–94% similar and diameter-class distributions were 87–88% similar to accurate plot estimates (Williams & Baker, 2011).

Reconstructions were represented by merged Voronoi polygons (Fig. 2), each based on a corner; these differ from the Voronoi polygons, each based on a single tree, used to estimate tree density. Corners were pooled using a 2:1 ratio of contiguous quarter corners to section corners, necessary as an unequal number of trees was recorded at each corner type (Williams & Baker, 2011). For reconstructing fire severity, parameters were combined into one feature with multiple attributes by an intersect analysis, which generally resulted in 2.6 km^2 polygons. The multiple attributes were then used to classify fire severity.

Section-line descriptions provide information on forest cover and understorey vegetation. Line descriptions, represented as linear transects of historical vegetation, were entered into ArcGIS exactly as recorded by surveyors. If no description was given, the line was coded as undescribed. Non-forested areas were excluded from this analysis.

Testing hypotheses

H_1: forest structure and composition

To test H_1, we used section-line descriptions and reconstructed tree density, diameter-class distributions and composition. For composition, we reconstructed the percentage of the landscape with: (1) ≥ 18% fir, the mean value of historical fir composition in models from the Blue Mountains (Hann *et al.*, 1997) and (2) ≥ 30% fir, near the upper limit from tree-ring reconstructions (Table S1). We also evaluated the section-line length for understorey trees and shrubs and distinguished lines described as 'dense' or 'scattered.' Forest parameters were summarized and visually examined using reconstructed maps to test hypotheses.

H_2: fire severity

Regarding H_2, age-structure and fire-scar data commonly used to reconstruct disturbance severity (Johnson & Gutsell, 1994) are not feasible for spatially comprehensive data such as the GLO surveys. However, forest-structure parameters (e.g. tree sizes) can be used to reconstruct the severity of disturbances that likely led to the forest structure (Oliver, 1981; Oliver & Larson, 1990; Lorimer & Frelich, 1998; Spies, 1998). We focus on fire as the primary disturbance agent in this forest type though forest structure cannot always distinguish fire from other agents, such as insect outbreaks (e.g., Hadley, 1994) or drought (e.g. Allen & Breshears, 1998). Structural reconstruction requires an assumption that tree size is generally related to tree age, and size-class structure and disturbance severity are linked (Spies, 1998). These assumptions have been shown to be sufficiently valid to allow reconstruction of low-, mixed- and high-severity fire from stand structure many decades after the event (Oliver, 1981; Lorimer & Frelich, 1998; Taylor & Skinner, 1998; Hessburg *et al.*, 2007), and this was independently verified in one study with tree-ring data (Stephens & Gill, 2005). Oliver (1981) classified stands into seral classes, each with characteristic mixes of tree size-structures. Hessburg *et al.* (2007) refined these classes and used them to reconstruct historical fire severity in eastern Washington, based on historical forest structure interpreted from early aerial photographs. Similarly, Taylor & Skinner (1998) used early aerial photos and stand structures to reconstruct historical fire severity in northern California.

To test hypothesis H_2, we similarly used stand structure to reconstruct fire severity, but with three improvements. First, we used reconstructions of stand structure at the time of the GLO surveys (*c.* AD 1880), rather than interpretations from aerial photographs taken several decades after Euro-American settlement. Second, we utilized multiple characteristics of quantified stand structure instead of visually estimated texture of height classes in aerial photos. Third, we calibrated our structure-based fire-severity definitions against tree-ring reconstructions. To do so, we analysed available tree-ring reconstructions to model the parameters of forest structure having historical low- and *higher*-severity (mixed- plus high-severity fire) fire regimes. We used 13 commonly cited studies with 55 tree-ring-based reconstructions or early plot estimates of historical forest structure in dry-forest areas identified by authors as dominated by low-severity fire (Table S1). We also used four studies with nine tree-ring-based reconstructions of historical forest structure in areas identified by authors as having either variable- (i.e. mixed-) or high-

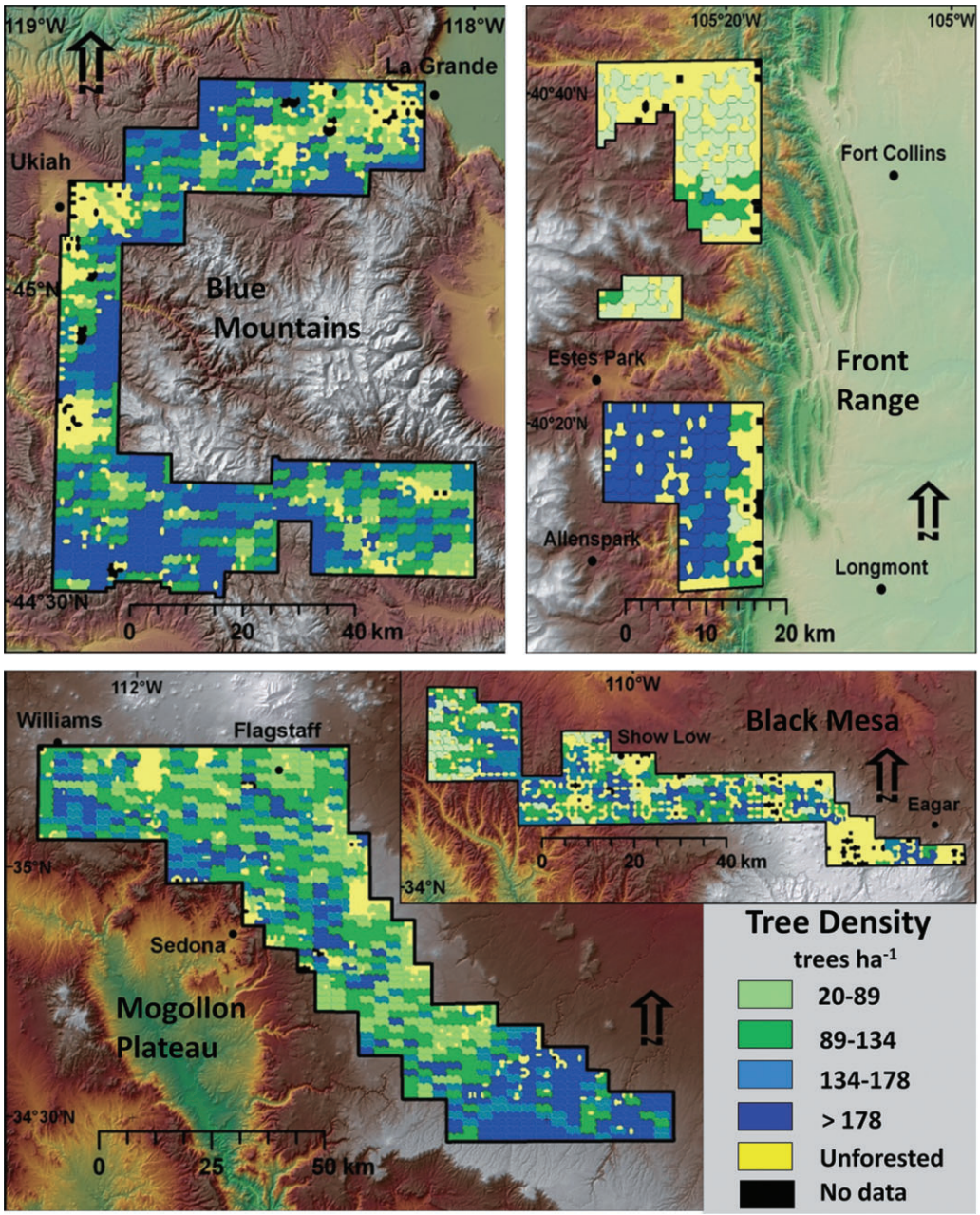

Figure 2 Historical tree density, based on survey reconstructions.

severity fire (Table S2). We were limited to studies with both diameter-class distributions and estimates of tree density.

Since low-severity fire is typically associated with low-density forests dominated by large conifers, and with few small conifers, we focused on these three forest-structure parameters, which can also be reconstructed from the GLO data: (1) tree density (all trees), (2) proportion of small (< 30 cm) conifers, and (3) proportion of large (> 40 cm) conifers (see Table 1). In the Colorado Front Range, tree growth is slower (Knowles & Grant, 1983) and we used < 20 cm for small and > 30 cm for large conifers. For low severity, we then accepted all areas within two standard deviations of model means for the three parameters and rejected areas not conforming to any one of the parameters. Thus, low-severity fire was assigned if: (1) mean tree density was < 178 trees ha^{-1}, (2) the percentage of large trees was > 29.2%, and (3) the percentage of small trees was < 46.9%. This definition spans the open, park-like old forests described in historical reconstructions (Covington & Moore, 1994), and virtually all low-severity fire areas identified by authors (Table S1).

To reconstruct *higher*-severity fire, we calibrated with tree-ring reconstructions in both known low- and *higher*-severity-fire areas (Tables S1 & S2). In reconstructions with lower-severity fire, the maximum percentage of small trees in any stand was 48.6% and the minimum percentage of large trees was

Table 1 A test of the low-severity model for forest landscapes in the western United States.

	Mogollon Plateau, AZ	Black Mesa, AZ	Front Range, CO	Blue Mountains, OR
Reconstruction area (ha)	405, 214	151,080	65,525	304,709
Parameters				
Parameter 1. Tree density: Percentage of forest with < 177.6 trees ha^{-1}	74.6%	76.7%	55.4%	65.2%
Parameter 2. Conifer diameter distributions for small trees: Percentage of forest where < 46.9% of conifer trees were < 30 cm	73.1%	20.0%	27.4%*	51.5%
Parameter 3. Conifer diameter distributions for large trees: Percentage of forest where > 29.2% of conifer trees were ≥ 40 cm	76.8%	29.7%	5.3%†	65.4%
Low-severity model: percentage of forest conforming to all three parameters	62.4%	12.0%	2.5%	40.3%

Notes: The low-severity model was based on 55 fine-scale tree-ring reconstruction plots or historical measurements from forests across the south-western United States and north-eastern Oregon. To determine the proportion of dry forests not conforming to the model, we calculated the percentage of the forest area where conditions deviated by more than 2 SD from the mean.

*Percentage of forest with trees ≤ 20 cm. Growth rates were lower in the Front Range; thus smaller diameters were used.

†Percentage of forest with trees > 30 cm. Growth rates were lower in the Front Range; thus smaller diameters were used.

28.8%. Since high severity should occur outside the range of forest structures assigned to low severity, high severity was defined as having a percentage of small trees > 50% and a percentage of large trees < 20%. This conservative definition identifies stands with few large survivors dominated by cohorts of small trees, consistent with past definitions of high-severity fire (Oliver & Larson, 1990; Taylor & Skinner, 1998; Hessburg *et al.*, 2007). Remaining areas, influenced by fires of moderate severity or a mosaic of different severities, were classified as mixed severity. Using these definitions, all tree-ring reconstructions (Table S2) in the *higher*-severity category would be correctly classified, except Flathead 1, which had a stand-replacement fire 300 years prior to the reconstruction date (Arno *et al.*, 1995; Table S2). For further local validation, we compared GLO-based fire-severity reconstructions with tree-ring estimates of fire severity at nine sites within or near our four study landscapes.

H_3: current and historical fire severity and disturbance rate

To test hypothesis H_3, we estimated fire rotation, the key rate parameter for fire regimes, as the number of years a fire was detectable divided by the percentage of the landscape burned by high-severity fire. The percentage of high-severity fire was based only on forested areas in each landscape, minus areas for which data were insufficient. We estimated the time a fire was detectable as the time it took for a tree to grow to the cut-off size for a 'large' tree. In northern Arizona, an average 40-cm tree is about 120 years old (Woolsey, 1911, Table 10 for ponderosa pine, n = 400), in Oregon's Blue Mountains, this same size is about 140 years old (Munger, 1917, Table 9, average age for ponderosa pine, n = 1081), and in the Colorado Front Range an average 30 cm tree is about 175 years old (Knowles & Grant, 1983, Fig. 5 for ponderosa pine, $r^2 = 0.26$, $n = 507$). These cut-offs appear to be the maximum length of time a fire could be recognized using this structure-based approach. For example, the Flathead fire (Table S2), a high-severity fire 300 years prior to reconstruction, was not detectable and a fire 150 years prior to reconstruction was barely detectable.

This method has some limitations and strengths relative to palaeofire estimates, which show substantial temporal variability in fire regimes (e.g. Pierce *et al.*, 2004). Tree growth rates are variable but cut-off tree sizes and ages are for average conditions, and the method is thus an approximation. It is also conservative, as multiple fires may have occurred in some areas. Fire-rotation estimates were from a single period, in which large fires could be missed or unusually severe fires could occur, leading to estimates that are too long or short. The method also uses only 120–175 years of data, less than the length of the estimated rotation. Nonetheless, these historical estimates are probably as good as modern ones based on only 24 years (Rhodes & Baker, 2008), which is the maximum period of published data. Moreover, these historical estimates are based on 927,000 ha of spatial data, a large sample area relative to palaeofire estimates.

Also regarding hypothesis H_3, historical landscape fire severity was compared with severity in recent large fires and

modern landscapes to test whether fire severity in dry forests has increased and is currently outside historic variability. We selected recent large fires that were considered unnaturally severe, within or near our reconstructed landscapes and large landscapes in dry forests reported in the literature. We also compared estimated historical high-severity fire rotation and recent high-severity rotation (Rhodes & Baker, 2008). Fire rotation was calculated assuming all parts of study areas could sustain high-severity fires, which is suggested by the wide distribution of high-severity fire and lack of barriers.

RESULTS

H_1: forest structure and composition

Reconstructed mean tree densities in the Front Range and Blue Mountains were 216.9 (median = 161.9, n = 145, s = 217.0) and 167.3 trees ha^{-1} (median = 146.2, n = 839, s = 89.8), respectively. Mean densities were lower on the Mogollon Plateau and Black Mesa at 141.5 (median = 124.3, n = 1131, s = 75.9) and 144.2 (median = 136.8, n = 342, s = 67.4) trees ha^{-1}, but still about 60% higher than estimates from tree-ring reconstructions (Table S1), which average 89.8 trees ha^{-1} (median = 81, n = 55, s = 43.9, for trees > 10 cm).

Large areas of lower-density forests did occur in all landscapes (Fig. 2), supporting density estimates from tree-ring reconstructions in these areas, but tree density was far from uniform. It is surprising that only about 33% of the Mogollon Plateau, 23% of the Black Mesa, 40% of the Front Range, and 23% of the Blue Mountains had open forests (i.e. < 100 trees ha^{-1}), and that large expanses of high density occurred. In the Front Range, 44.6% of the landscape had > 200 trees ha^{-1} and 37.5% had > 250 trees ha^{-1}. In Oregon's Blue Mountains, 28.9% and 16.6% of the landscape had > 200 and 250 trees ha^{-1}, respectively. Arizona forests were less dense, but 15.3 to 16.7% of the two historical landscapes still had > 200 trees ha^{-1}.

For section-line data, in Arizona our reconstructions show that < 2% of these landscapes had > 18% firs (Table S3). However, in the Blue Mountains, 42.9% and 19.3% of the landscape had > 18% and > 30% firs, respectively; in the Front Range, values were 36.0% and 26.9%. Also, outside Arizona, firs were widely distributed. Firs were present in only 7.0 and 7.9% of stands on the Mogollon Plateau and Black Mesa, respectively, but were found in 36.6 and 83.4% of stands in the Front Range and Blue Mountains, respectively.

The Mogollon Plateau and Black Mesa had 7–10% of understoreys with small trees and 7–11% with shrubs. The Front Range had sparse (only 2.5%) understorey shrubs and small trees. However, understorey shrubs or small trees occurred on 41% of the Blue Mountains' landscape, and the majority was described as dense (Table S3).

H_2: historical fire severity

Structural evidence of past high-severity fire was most common in the Front Range (64.6%) and on Black Mesa (55.2%), and less so but still notable on the Mogollon Plateau (14.5%) and in the Blue Mountains (16.5%) (Fig. 3, Table 2). Evidence of mixed-severity fire was most common in the Blue Mountains (43.2%). On the Mogollon Plateau, 62.4% of the landscape was dominated by low-severity fire, including the northern plateau where many tree-ring reconstructions occurred (Abella & Denton, 2009). The validity of our structure-based method is supported, as it accurately estimated the severity of fires for all nine tree-ring-based studies within and near our study areas, at spatial scales from 518–3022 ha (Table S4).

Fire severities from other historical landscape estimates were comparable to our estimates (Table 2). For the Front Range estimate, Sherriff & Veblen (2007) found that about 20% of the dry-forest landscape was primarily influenced by low-severity fire and 80% was affected by *higher*-severity fire. The landscape of the eastern Cascades (Hessburg *et al.*, 2007) most closely compares with the Blue Mountains. The amount of high-severity fire found by Hessburg *et al.* (2007) was essentially equivalent to ours, but they found more mixed-severity and less low-severity fire than in our reconstruction.

H_3: current and historical fire severity and fire rotation

Estimated fire rotations for the Mogollon Plateau and the Blue Mountains were 828 and 849 years, respectively. For the Black Mesa and the Front Range, where high-severity fire was more common, rotations were 217 and 271 years, respectively. Combining the two adjacent landscapes in Arizona yielded a high-severity fire rotation of 522 years. The recent high-severity fire rotation in ponderosa pine forests in the central and southern Rockies (Front Range) is 714 years, in the south-west (Mogollon and Black Mesa) it is 625 years, and in the north-west (Blue Mountains) it is 1000 years (Rhodes & Baker, 2008). These modern rates of high-severity fire are all lower (longer rotation) than our estimates of historical fire rates.

Comparing past and present fire severity, a prominent recent fire, the Rodeo-Chediski (2002), overlapped the Black Mesa landscape. The *higher*-severity portion of this fire was 68.3%, almost 20% lower than the estimated historical landscape *higher*-severity area of 88% (mixed 32.8% plus high 55.2%, Table 2). The more recent Wallow Fire (2011) also occurring on Black Mesa, had only 15.6% high severity. In another prominent fire, the Hayman (2002) in the Colorado Front Range south of our reconstruction area, the *higher*-severity portion was 45.8% compared with 97% for the historical landscape. The two fires in the Blue Mountains have a slightly larger percentage of high-severity fire but a much lower percentage of mixed-severity fire (Table 2).

DISCUSSION

H_1: forest structure and composition

Three findings from our reconstructions bear on H_1. First, reconstructed tree density shows that dry forests commonly

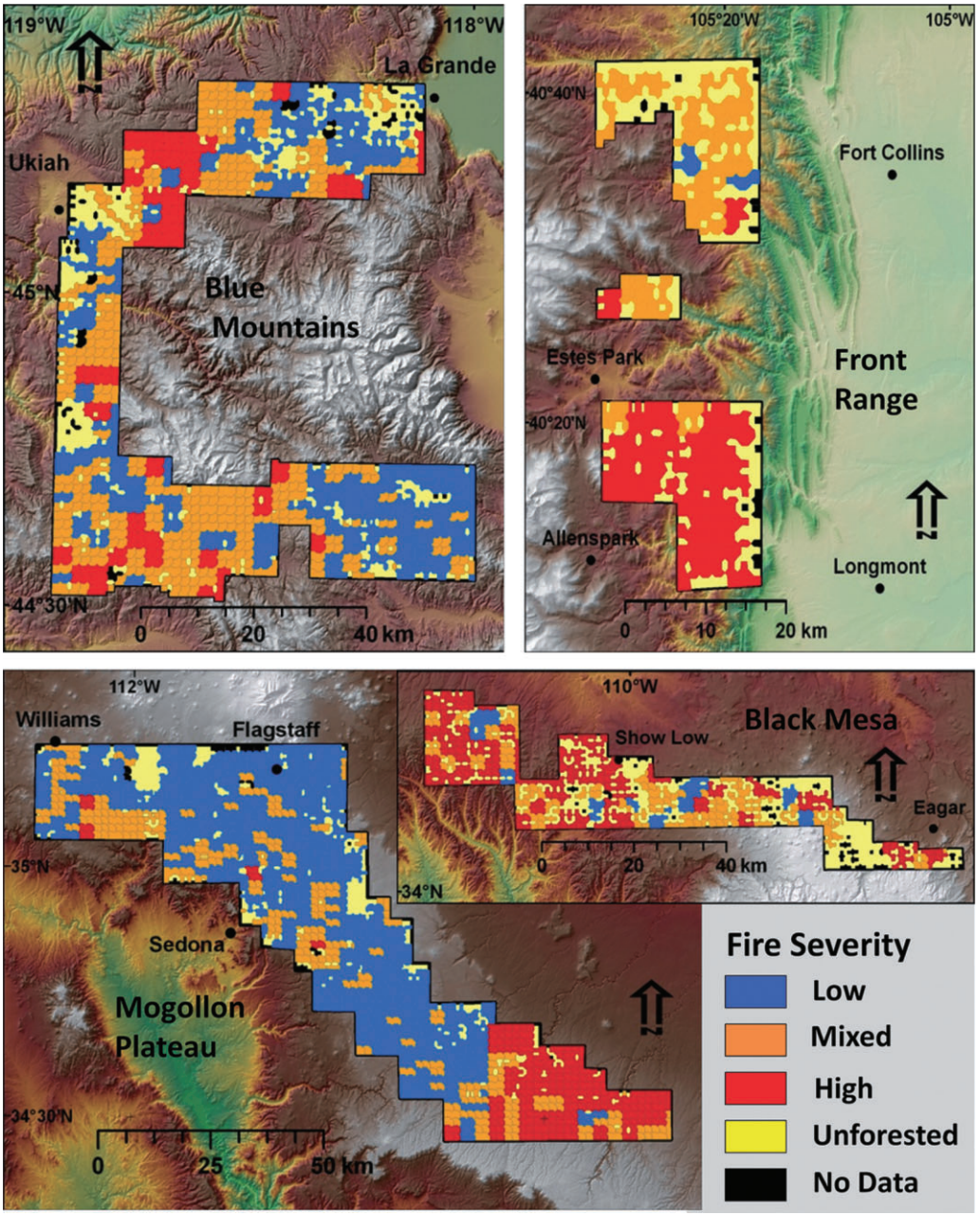

Figure 3 Fire-severity evidence from forest structure, based on survey reconstructions.

thought to have been open and park-like (i.e. < 100 trees ha^{-1}) instead had higher historical mean tree densities and large areas of dense trees (Fig. 2). Second, shade-tolerant firs, considered historically uncommon in dry forests (Keane *et al.*, 1990; Hann *et al.*, 1997), were common in some landscapes but uncommon in the south-west. Widespread distribution and the substantial composition of firs in many forests, particularly outside Arizona, show that low-severity fire did not historically keep firs rare in these landscapes. Third, shrubs and small trees, also considered rare because of frequent fires, were common in places (Table S3). Low-severity fire, at least in the Blue Mountains but to some extent also in Arizona, did not keep shrubs and small trees rare.

Thus the evidence rejects H_1, that forests were uniformly park-like and similar in composition. Our study landscapes span the large distributional range of this forest type and some inherent differences in structure and species composition can be expected from this alone. However, rather uniform restoration treatments are typically conceived (e.g. the Healthy Forests Restoration Act of 2003). Although some large areas within each landscape were fairly homogeneous, even on the Mogollon Plateau only 62% of the landscape fits the low-severity fire paradigm, suggesting that more heterogeneous management is warranted across each landscape. Other recent reconstructions (Stephens & Gill, 2005; Brown & Cook, 2006) have also found heterogeneous forest structure, strengthening our findings.

Table 2 Historical fire severity compared to modern fire severity in dry western forests.

	Unburned to low§	Low (%)	Mixed (%)	High (%)
Historical fire severity – our study areas				
Mogollon Plateau, AZ (405,214 ha)		62.4	23.1	14.5
Black Mesa, AZ (151,080 ha)		12.0	32.8	55.2
Front Range, CO (65,525 ha)		2.5	32.9	64.6
Blue Mountains, OR (304,709 ha)		40.3	43.2	16.5
Historical fire severity – other study areas				
Front Range, CO (60,875 ha)*		18.7		81.3
Eastern Cascades, WA/OR (112,115 ha)†		21.6	58.6	19.8
Modern fire severity – individual fires‡				
Rodeo-Chedeski, AZ (186,866 ha)	15.1	16.6	31.7	36.6
Wallow, AZ (217,741 ha)	25.0	42.9	16.5	15.6
Hayman, CO (53,212 ha)	42.8	11.4	24.3	21.5
Huckleberry, OR (3,257 ha)	23.6	31.5	26.0	18.9
Sunflower, OR (3,442 ha)	30.7	25.1	22.0	22.2

*Sherriff & Veblen (2007).
†Based on dry forests (Hessburg *et al.*, 2007, Table 3).
‡All modern estimates of fire severity are from the US government (http://www.mtbs.gov) except the Wallow Fire which is from the Burned Area Emergency Response (BAER) team maps available on (http://activefiremaps.fs.fed.us/baer/download.php). BAER maps are based on changes in soil reflectance.
§Fire severity is classified into four categories by Monitoring Trends in Burn Severity (http://www.MTBS.gov), and low severity is split into 'Unburned to low' and 'Low'.

H_2: historical fire severity

Severity estimates from structural data show that the low-severity fire model commonly fit portions (62%) of the Mogollon Plateau but less commonly fit other landscapes (Table 1, Fig. 3). Thus, we reject H_2, as a low-severity fire regime was prevalent in only part of the dry forest landscape and *higher*-severity fire was common in all landscapes, even in the south-western USA where the low-severity model was developed (Table 2). Dry forests in the western USA with evidence of *higher*-severity fire probably had a variable-severity fire regime in which periodic low- or moderate-severity fires occurred with more infrequent high-severity fire (Veblen *et al.*, 2000; Baker *et al.*, 2007; this paper). Variable-severity regimes also include areas categorized as mixed-severity, where fires might burn at any severity level dependent on fuel structure and climate (Sherriff & Veblen, 2007).

A dry-forest landscape with evidence of widespread *higher*-severity fire would not necessarily be devoid of trees, as often interpreted, as these fires may only partially kill trees and occur infrequently, over hundreds of years. For high-severity fire, 70% or more of the trees or basal area are killed or removed (Hessburg *et al.*, 2007). If pre-fire density was 200 trees ha^{-1}, up to 60 trees ha^{-1} could remain on the landscape after a single fire. In fact, for the Colorado Front Range, where 80–97% of the forest was influenced by *higher*-severity fires, one study found 70% of stands had some trees > 200 years old and 30% had trees > 400 years old, a substantial amount of old growth (Huckaby *et al.*, 2001). *Higher*-severity fire could also at times leave openings or shrub fields caused by multiple fire events, which was not an unnatural occurrence (e.g., Jack, 1899).

H_3: current and historical fire severity and disturbance rate

All the modern fires examined that were previously considered anomalously severe (Graham, 2003; Strom, 2005) appear to be within the range of historical variability based on the historical reconstructions of severity (Table 2). Indeed, even if these fires occurred repeatedly, they likely could not produce the level of *higher*-severity fire found in historical landscapes. Modern estimates of high-severity fire rotation, based on fire records, were all longer than historical reconstructions from forest structure. The hypothesis that recent high-severity fire rotations are shorter in the last three decades than historically was not validated. Consequently, the recent fraction of high-severity fire is not unprecedented and has not increased, relative to the historical record, and hypothesis H_3 is rejected.

From a longer perspective, this finding may not be surprising, as fire regimes in dry western forests have been shown to vary over centennial to millennial time-scales and to include some episodes of high-severity fire (Pierce *et al.*, 2004; Jenkins *et al.*, 2011). Climate influences much of this variability by directly influencing the type and amount of vegetation or fuel and by creating dry conditions which increase the likelihood of fire and its potential severity (Colombaroli & Gavin, 2010). Temporal variation in burning, even in the era of fire suppression, can

largely be explained by climate (Trouet *et al.*, 2006). However, spatially extensive evidence of historical *higher*-severity fire has been lacking. Other evidence of some historical *higher*-severity fire in our study landscapes can be found in forest-reserve reports, early scientific journals, the palaeoecological record and tree-ring studies (see Appendix S1 for a more in-depth examination).

Limitations of structural-based reconstructions

It has been logically argued that the use of static forest structure can result in misinterpretation of forest dynamics (Johnson *et al.*, 1994). For example, it is well established that climate has a strong influence on long-term forest dynamics (e.g. Pierce *et al.*, 2004; Colombaroli & Gavin, 2010). One critique of structurally reconstructed fire severities is that structure may also be shaped by site quality, physiography, climate and tree physiology (e.g. Everett *et al.*, 2008). Although a single forest characteristic may partly reflect site conditions (e.g. Abella & Denton, 2009), a combination of characteristics, including multiple tree sizes and/or tree density, allows for more complex inference.

One example of the structure–dynamics ambiguity for dry western forests deals with defining high-severity fire for stands having only a small number of large old trees (< 20%) and many small trees (> 50%). Some authors have suggested these stands result when widespread drought or insect outbreaks are followed by a fire-free period under pluvial conditions, which induces a cohort of regenerating trees (e.g. Brown & Cook, 2006). Other authors explain that these stands were located on marginal sites and, during favourable climatic conditions, a cohort of trees developed (Everett *et al.*, 2008).

We analysed these possible alternative hypotheses including higher-severity fire for the combined high-severity regions in all four landscapes, which is 188,929 ha. In this area, the reconstructed mean percentage of small trees was 73.0% ($n = 578$, $s = 10.5\%$), the mean percentage of large trees was 10.8% ($n = 578$, $s = 5.9$) and the mean density of large conifer trees was only 21.3 trees ha^{-1} ($n = 578$, $s = 15.1$). Compared with the reconstructed mean density of park-like stands of 89.8 trees ha^{-1} with 56.6 large trees (Table S1), 21.3 trees ha^{-1} would be a 62.4% reduction, close to the 70% reduction identified as the threshold of high-severity fire (assuming equal reduction in basal area, Hessburg *et al.*, 2007), thus indicating possible high-severity fire. Regarding the marginal-sites hypothesis, given the large area and high percentage of high severity in some landscapes (up to 64.6%), it is very unlikely that such widespread high-severity areas represent marginal sites where tree density was naturally low because of site conditions (Everett *et al.*, 2008). Additionally, tree growth rates were not found to be lower in high-severity areas (e.g. Black Mesa: Woolsey, 1911).

The drought/irruptive cohort hypothesis also fails to provide a satisfactory explanation. If region-wide pluvial conditions caused irruptive cohorts, why would they not be present uniformly and in a high percentage of historical stands? There were certainly many areas of historical low-density stands with suitable sites for tree establishment (Shepperd & Battaglia, 2002). For example, on the Mogollon Plateau, 33.4% of the forest had low tree density (i.e. < 100 trees ha^{-1}). If irruptive cohorts occurred, why was only 16.9% of the forest influenced while the remaining 83.1% was not? Moreover, a short distance away (< 50 km) on Black Mesa, a much greater amount of the landscape (55.2%), was influenced and 44.8% was not. The irruptive-cohort hypothesis does not fit the spatial extent and variability in these patterns.

Regeneration of trees after a *higher*-severity fire poses another limitation to our structure-based methods as recruitment of ponderosa pine and other species can be irregular and highly variable (Baker *et al.*, 2007). Although not serotinous, most ponderosa pine regeneration occurs within 30 years after a fire event but in some cases, regeneration may be delayed up to 150 years (Huckaby *et al.*, 2001; Ehle & Baker, 2003; Baker *et al.*, 2007). Therefore, we may miss some high-severity events. The structure-based approach can only identify disturbances at some lag time after the event has occurred, following recruitment and tree growth and then only up to the time where trees reach large size (i.e., 40 cm).

CONCLUSION

These spatially extensive reconstructions of forest structure and fire severity show, for the first time, the substantial spatial heterogeneity in historical dry-forest landscapes that were commonly thought to have been rather uniform. Variable-severity fires, including substantial high-severity fire, interacted with the variation in environmental setting over long time periods (e.g. Hessburg *et al.*, 2007), to produce these structurally diverse dry-forest landscapes. Common management practices today include extensive, rather uniform reduction in tree density, removal of understorey shrubs and small trees, and other fuel modifications to lower fire severity. Our reconstructions show that these common practices, if widespread, will move most dry forests outside their historical range of variability, rather than restore them, probably with negative consequences for biological diversity (Keane *et al.*, 2009).

Survey-based reconstructions overcome the inherently limited spatial detail in tree-ring and palaeoecological studies, to provide a spatially explicit, macroscale frame of reference for restoring landscapes, but limited to a single key time period before widespread Euro-American land use. However, when survey-based and palaeoecological studies (e.g. Pierce *et al.*, 2004) are combined, together they show that, if the goal is to perpetuate native biological diversity, it is appropriate to restore and manage for spatial and temporal variability in forest structure and fire severity, including substantial areas of dense forests and high-severity fire, across dry western forests in the United States.

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SUPPORTING INFORMATION

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

Table S1 Reconstruction studies and data on which the low-severity model is based.
Table S2 Reconstruction studies and data on which *higher*-severity models are based.
Table S3 Historical forest overstorey and understorey summaries in dry forest.
Table S4 Test of General Land Office (GLO) methods to estimate historic disturbance severity.
Appendix S1 Supplementary data – supporting evidence of *higher*-severity fire.

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