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Landscape restoration of a forest with a historically mixed-severity fire regime: What was the historical landscape pattern of forest and openings?

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ABSTRACT

Forest management of dry forests in the western US that historically experienced mixed-severity fire regimes is increasingly focused on landscape-scale restoration. However, this restoration effort is constrained by historic range of variation (HRV) reference conditions that lack information concerning the spatial configuration of these forests at intermediate scales (approximately 0.01–100 ha). I used reconstruction methods to map historical (1860) pattern of ponderosa pine-Douglas-fir forests along twenty 1 km long transects on Colorado's Front Range and compared pre-settlement opening and forest patch lengths to current forest configurations to inform restoration reference conditions. Historically, openings were prevalent on south-and east-facing aspects, at lower elevations, and on gentler slopes. Generally, mean forest cover rose from 57% prior to settlement to 83% currently, and the current condition of any one location is 3.7 times more likely to be forested now than prior to settlement. In addition, the mean forest patch length increased from 35 to 118 m long. However, the mean opening length has changed little, increasing from 26 to 27 m long. Changes in the distribution of forest opening lengths suggest that there has been a loss of small openings (<50 m long) producing the small increase in mean patch length; however, the abundance of larger openings (>50 m) across the landscape has been relatively stable. In addition, there has been an increase in large forest patches (>50 m) at the expense of small forest patches (<50 m). Results from this study suggest that forest restoration treatments should focus on recreating small openings (<50 m long) by breaking up large contiguous forest canopy patches within the context of local site conditions.

1. Introduction

The structure and function of dry forest ecosystems of the western United States have changed since European American settlement in the late 19th century, and generally these forests are currently more susceptible to large severe wildfires than they have been historically (Allen et al., 2002; Noss et al., 2006). To address these issues, forest managers are increasingly applying landscape ecology theories to inform silvicultural treatments; however, there is generally a paucity of information regarding the landscape-scale structure and function of these ecosystems.

For example, the montane ponderosa pine (*Pinus ponderosa*) forests of Colorado's Front Range have changed since European American (*circa* 1860) settlement due to historical logging, grazing and fire suppression (Gruell, 1985; Kaufmann et al., 2000, 2003; Marr, 1961; Mast et al., 1998; Sherriff and Veblen, 2006; Veblen and Donnegan, 2005; Veblen and Lorenz, 1986, 1991; Veblen, 2000). While historically these forests were maintained by a mixed-severity fire regime (Brown et al., 1999; Sherriff and Veblen, 2006, 2007; Veblen et al., 2000; Veblen and Lorenz, 1986), the increase in forest density accompanied by the increasingly warm and dry climate have led to undesirably large and severe wildfires on the Front Range in recent decades (e.g., Black Tiger Fire in 1989, Buffalo Creek Fire in 1996, Hi Meadow and Bobcat Gulch Fires in 2000, Hayman Fire in 2002, Four Mile Canyon Fire in 2010, Hewlett Gulch, High Park and Waldo Canyon Fires in 2012, and Black Forest Fire in 2013). Similar changes in disturbance regimes and forest structure have also occurred in

Abbreviations: HRV, Historic range of variation; FR-CFLRP, Front Range Collaborative Forest Landscape Restoration Project.

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other fire-adapted coniferous forests that historically demonstrated low- and mixed-severity fire regimes across the western US (Allen et al., 2002; Noss et al., 2006).

Because of this increased occurrence of undesirable wildfire, forest managers are increasingly focusing on manipulating the structure of these forests at the stand- and landscape-scales with the aim of mimicking or restoring the historical fire regime (Covington, 2000). Typically, these treatments use thinning techniques to reduce canopy fuel loads and break up the continuity of horizontal and vertical fuel complexes to modify fire behavior (Hunter et al., 2007). Forest managers are also seeking to improve wildlife habitat and the diversity of understory plants by reducing forest canopy cover and increasing the structural diversity of the forest (FRLRI, 2010).

In the absence of comprehensive context-specific information about primeval ecosystem functioning of these forests, forest managers have turned their focus to using the forest structures and compositions that existed prior to settlement as reference conditions (Keane et al., 2009; Veblen and Donnegan, 2005). The hope is that this restoration of forest structure and composition will promote sustainable ecosystem function. Specifically, by incorporating elements of pre-settlement forest structures, these managers aspire to recreate fuel complexes similar to those prior to settlement and therefore return the historical disturbance regime. Therefore, the focus of many forest managers has been to create a "natural-looking" heterogeneous landscape with varying proportions of tree groups, openings and single isolated trees among stands (Abella and Denton, 2009; Churchill et al., 2013; Larson and Churchill, 2012).

However, due to the paucity of published studies that quantify the historical landscape-scale forest structure at intermediate scales (approximately 0.01–100 ha) uncertainty and debate surround the reference conditions for restoration, particularly for forest types that historically maintained a mixed-severity fire regime. For example, forest managers working to restore montane ponderosa pine forests on Colorado's Front Range frequently ask "How large should forest openings be?" and "How big should the residual patches of forest be?" Currently, there is limited scientific basis to determine the likely pre-settlement size of these openings and forest patches in these forests, or provide guidance about the appropriate spatial configuration of forest restoration treatments.

A number of studies in the dry forest ecosystems of the western United States have examined the historical fire regime to inform restoration using a range of techniques. Dendrochronological studies of fire scars have been used to reconstruct historical fire frequency and extents (e.g. Brown et al., 1999; Sherriff and Veblen, 2007); however, these studies provide limited information about the appropriate size of openings or forest patches for restoration. Further studies have investigated the fine-scale (<10 m) patterns of trees using point pattern analyses (e.g. Mast and Veblen, 1999), but do not provide information regarding coarser-scale landscape patterns. In addition, studies using early land survey records utilize spatially sparse data and therefore may inform managers regarding broad-scale regional patterns (e.g. Williams and Baker 2012a,b); but, are known to have a number of limitations (Fulé et al. 2013; Schulte and Mladenoff, 2001).

A handful of studies have specifically reconstructed the historic spatial configuration of various dry forest ecosystems in North America. These studies encompass a wide range of forest types, with varying historic fire regimes and opening or forest patch sizes ranging from 6.6 m^2 to 3373 ha (Fry et al., 2014; Lydersen et al., 2013; Stephens and Fry, 2005; Skinner, 1995). In terms of forests dominated by mixed-severity fire regimes specifically, Agee (1998) suggested that these fire regimes may result in a great variety of opening sizes ranging from 0.1 to 300 ha. In contrast, Hessburg et al. (2007) detected a range of forest patch sizes from 4 to 3373 ha using early aerial imagery in eastern Washington. While, Kaufmann et al. (2000) determined that historically forest openings ranging in size from <1 ha to >20 ha probably accounted for 10–20% of the Cheesman Reservoir landscape on Colorado's Front Range prior to settlement.

In addition, a number of spatially-explicit studies of forest ecosystems dominated by mixed-severity fire disturbance regimes have also demonstrated an approximately "reverse-J" distribution of land-cover patch sizes across the landscape, with many small patches that cumulatively occupy a small proportion of the area and few large patches that cumulatively occupy the majority of the landscape (Halofsky et al., 2011; Perry et al., 2011; Collins and Stephens, 2010; Hessburg et al., 2007). Similar distributions have been demonstrated in forests dominated by low-severity fire (Fry et al., 2014; Stephens and Fry, 2005; Piirto and Rogers, 2002; Skinner, 1995; Lydersen et al., 2013) and high-severity fire (Johnson et al., 1998) disturbance regimes.

Whilst these studies inform forest restoration, further information is needed to guide restoration treatments in dry forest ecosystems with historically mixed-severity fire regimes, particularly in terms of opening size and location.

The objective of this study was to investigate the current and historical landscape configuration of montane ponderosa forests that were historically dominated by a mixed-severity fire regime prior to settlement at intermediate scales (approximately 0.01–100 ha), to inform forest restoration activities. Furthermore, it is hoped that this study may provide insight into the historical landscape configurations of dry forests dominated by mixed-severity fire regimes generally. Specifically, I sought to answer the following questions:

1. How open was the montane ponderosa forest on Colorado's Front Range prior to settlement compared to current conditions, and how did forest patches and openings vary with topographic gradients such as slope, aspect and elevation?
2. What was the size distribution of forest patches and openings in montane ponderosa forests of Colorado's Front Range prior to settlement compared to current conditions?

I hypothesize that forest cover in these montane ponderosa forest cover has increased since settlement at the expense of forest openings. In addition, I expect that prior to settlement, openings were more prevalent on drier (south-facing, low elevations) than more mesic sites (north-facing, higher elevations).

Furthermore, I hypothesize that montane ponderosa forests on Colorado's Front Range will exhibit a "reverse-J" distribution of patch sizes similar to those demonstrated in studies elsewhere (Halofsky et al., 2011; Perry et al., 2011; Collins and Stephens, 2010; Hessburg et al., 2007). In addition, I hypothesize that there has been a reduction in the number of large openings since settlement through the incursion of forest regeneration from adjacent forest patches and that the "filling in" of small openings by the invading forest has reduced the abundance of small openings.

To test these hypotheses, I mapped current forest cover and evidence of pre-settlement forest cover (old trees, stumps and eroded coarse woody debris) along extended transects across the landscape, and investigated the lengths of these patches and openings prior to settlement and currently.

2. Materials and methods

2.1. Study sites and data collection

The Arapaho-Roosevelt and Pike National Forests are actively restoring montane ponderosa pine and dry-mixed conifer forests as part of the Front Range Collaborative Forest Landscapes

Restoration Project (FR-CFLRP). Therefore, to inform planned restoration activities, five transects were established at each of four sites within these two national forests (two sites at each of the national forests; Fig. 1 and Table 1). All of these sites are located in the montane zone of Colorado's Front Range, and are dominated by ponderosa pine (*P. ponderosa)*-Douglas-fir (*Pseudotsuga menziesii*) forests.

A pool of random potential transects was created using GIS by generating 100 random starting points within each of the four 220–330 ha sites, and plotting 1 km long transects from each starting point using random azimuths. The first five transects at each site that satisfied the following criteria were selected. Potential transects that crossed onto private land were excluded from the study as I did not have permission to access this land. In addition, potential transects that crossed areas of known recent disturbances such as wildfire or silvicultural treatments were excluded as it is likely that these disturbances would remove evidence of historical structure. Furthermore, potential transects that crossed into areas of non-forest land use were excluded (e.g. agricultural land). Potential transects that crossed meadows and rocky outcrops within forests were not excluded.

In the field, a GPS and compass was used to locate the starting point and direction of each transect. Each 1 km transect was composed of contiguous 100 m^2 quadrats (10 m × 10 m), with a total of 100 quadrats per transect (Fig. 2). Within each quadrat, the evidence of forest cover prior to European American settlement (1860) and current forest cover were noted (irrespective of tree size). Specifically, the presence of old (>200 years) and transitional (150–200 years) ponderosa pines was noted using morphological traits (Huckaby et al., 2003). Old trees were identified by their flattened, sparse and open ("bonsai") crown shapes with large branches high in the crown; small crown ratio (due to natural pruning from the historic fire regime); columnar trunk shape; characteristic orange smooth or small flaky bark; and fire scars, dead tops and broken branches, lightning scars, burls, and "cat faces" (Huckaby et al., 2003). While old trees may not exhibit all of these traits, a preponderance of these characteristics is a good indicator that the tree is >200 years old (Huckaby et al., 2003). In contrast, transitional and young ponderosa pines tended to have pointed conical or ovoid crown shapes; tapered trunks; deeply fissured gray bark; an absence of fire scars, dead tops and broken branches, lightning scars, burls, or "cat faces" (Huckaby et al., 2003). Tree cores were collected and aged in the field from a subset of ponderosa pine trees to confirm the tree's age. In addition, tree cores were collected and aged in the field from other tree species, such as Douglas-fir, which do not have easily identifiable morphological characteristics linked to tree age.

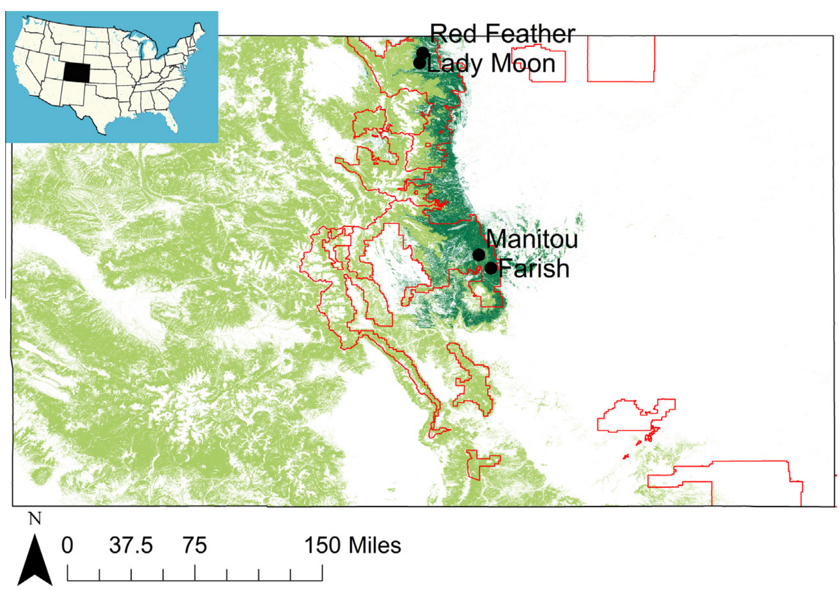

Fig. 1. Map showing the location of the four study sites (filled black circles) within Colorado (state boundary outlined in black). Inset map (top left) shows location of Colorado (black) within the United States. Light green shading indicates the location of Colorado's forests (Fry et al., 2011), while dark green shading indicates the location of montane ponderosa pine and dry mixed conifer forests on the Front Range (Landfire, 2014). Red outline is the extent of Arapaho-Roosevelt National Forest and Comanche Grasslands; and Pike-San Isabel National Forests and Pawnee Grasslands. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Table of site characteristics including the national forest, percent slope, elevation, current basal area, current ponderosa pine basal area and current Douglas-fir basal area. The full range of plot values is given, with the mean value for the site in parentheses.

Site	National Forest	Slope (%)	Elevation (m)	Current basal area (m^2/ha)	Current ponderosa pine basal area (m^2/ha)	Current Douglas-fir basal area (m^2/ha)
Farish	Pike	1.3–75.4 (24.9)	2616–2843 (2769)	0–45.9 (22.5)	0.5–41.3 (5.5)	0–32.1 (9.2)
Lady Moon	Arapaho-Roosevelt	2.2–57.8 (11.8)	2488–2683 (2571)	0–64.3 (8.9)	0–29.8 (4.3)	0–16.1 (1.0)
Manitou	Pike	0.3–63.2 (22.3)	2328–2745 (2559)	0–59.7 (22.5)	0–29.8 (5.1)	0–43.6 (8.5)
Red Feather	Arapaho-Roosevelt	0.1–60.7 (16.8)	2360–2547 (2426)	0–64.3 (9.3)	0–64.1 (7.0)	0–18.4 (1.1)

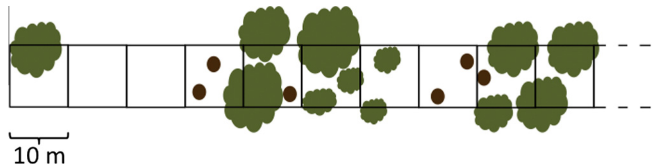

Fig. 2. Illustration of transect design. 100 contiguous quadrats, each 100 m^2, were arranged to form a 1 km transect (10 quadrats shown, black lines). The presence of current forest cover, and sign of pre-settlement forest cover (old trees, stumps and eroded coarse woody debris) were also noted. Green filled shapes are individual tree crowns and brown filled circles indicate eroded stumps or coarse wood. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Furthermore, the presence of tree remnants (stumps, snags and coarse woody debris) that likely originated from trees that were alive prior to settlement was noted. Eroded cut stumps (containing only heartwood) were assumed to be harvested at some time after settlement (1860) but would have resulted from the harvesting of trees that were extant prior to settlement (Brown and Cook, 2006; Brown et al., 2012). Similarly, other eroded coarse woody debris was likely to be derived from trees that were extant prior to settlement (Brown and Cook, 2006; Brown et al., 2012). Other stumps and coarse woody debris with bark and/or sapwood in addition to heartwood were generally rare because the study sites specifically excluded sites of recent harvesting; however, where present the status of the tree at time of settlement was determined by estimating the time since disturbance and age of the tree at death considering the state of decay, tree morphological traits (described above) and field counts of tree rings (where possible). Lastly, the presence of current forest cover (tree boles) in each quadrat was noted, the current basal area by species for each quadrat estimated using a BAF prism and a GPS location for the center of the quadrat recorded.

Using the data collected, the length of current and pre-settlement forest patches and openings was calculated to the nearest ten meters by multiplying the number of contiguous quadrats by 10 m (the width of the quadrats). Therefore, expanded openings (bole to bole) from 10 m long (i.e. a single 10 × 10 m quadrat) up to >1 km long are detectable.

2.2. Data analysis

To contrast the historical and current forest openness and examine how this varies across topographic gradients, each quadrat within the twenty transects was treated as an individual sampling unit. The proportion of quadrats with and without forest cover, prior to settlement and currently, were calculated to determine a non-spatial measure of forest openness. To test if the forest cover and time period variables were independent, and therefore whether the openness of the landscape differed between pre-settlement and current conditions, a Fisher's exact test was then used. The odds ratio was also calculated as an indicator of the changes between pre-settlement and current conditions.

In addition, slope, aspect (North, South, East or West), topographic curvature (profile, planform and overall), and elevation of each quadrat on the transects were derived from digital elevation models in ArcGIS. Profile curvature is parallel to the direction of the maximum slope, with positive values indicating a convex slope while negative values indicate a concave slope, and zero indicates a linear surface. In contrast, planform curvature is perpendicular to the direction of maximum slope, with positive values indicating a sideways convex fan while negative values indicate a sideways concave cirque-like shape. Overall curvature combines both profile and planform curvature. Logistic regression was used to test whether these factors were statistically predictive of the presence of forest cover prior to settlement, and currently. Initially, slope, elevation, topographic curvature (overall) and aspect were included in the logistic regression model as fixed factors, and site was included as a block factor. Where overall topographic curvature was significant, the logistic regression was repeated with planform and profile topographic curvature used instead. To calculate the overall significance of the categorical independent variables (aspect and site), a follow-up Wald test was used.

The length of each forest patch or opening was calculated to determine the size distribution of patches and openings on each transect. Lengths were estimated as the number of contiguous quadrats with either forest canopies or openings, multiplied by the quadrat width (10 m). Shapiro–Wilk normality tests on the distribution of pre-settlement and current openings and forest patch lengths indicated they were not normally distributed (all p-values <0.001). Therefore, I used non-parametric tests to detect differences.

Variation in opening and forest patch lengths among the sites in terms of pre-settlement opening, pre-settlement forest patch, current opening and current forest canopy patch lengths was tested using a rank transformed ANOVA of the median, 1st and 3rd quartiles for each transect. A rank transformation was used due to the skewed non-normal distribution of forest patch and opening lengths; however, this transformation does not alleviate concerns regarding the unequal sample sizes resulting from the skewed distribution. Therefore, the median, 1st and 3rd quartile of forest patch or opening length were calculated, and tested using a rank transformed ANOVA. The sample unit was the median, 1st and 3rd quartile of forest patch or opening length for each transect ($n = 60$), and site was the only variable included in the ANOVA model.

In addition, a rank transformed ANOVA was used to test whether the mean forest patch or opening length differed between pre-settlement and currently. Again, the sample unit was median, 1st and 3rd quartile of forest patch or opening length for each transect ($n = 60$); however, both site and time period (pre-settlement or current) were included as factors in the ANOVA model.

I hypothesized that the distribution of forest patches and openings differs today from pre-settlement conditions. Therefore, I tested whether the distribution of patch or opening lengths was different in the pre-settlement forest compared to currently by using two-sample Kolmogorov–Smirnov tests. The sample unit was the patch or opening length, with the pre-settlement distribution contrasted with the current distribution.

Finally, to test whether the frequency distribution of openings and forest patches fitted a "reverse-J" size distribution and further investigate differences in the distribution of the patch and opening sizes prior to settlement and currently, I fitted a negative power function ($y = b_0 + b_1x^{-2}$; where y = frequency, and x = patch or opening length). The negative power function was used as it has the "reverse-J" shape of a decay curve, with the high frequency of small values and relatively few large values. The regression coefficients of the current and pre-settlement size distributions could then be compared using t-tests. All statistical analyses were performed using R version 2.15.3 (R Core Team, 2013) with a significance value (α) of 0.05.

3. Results

Time period (pre-settlement or current) and the presence of forest cover are not independent, with a Fisher's exact test of independence p-value of <0.001 (Table 2). Furthermore, the odds ratio is 3.65 (95% confidence interval of 3.48–3.83) suggesting that the current condition of the cell is 3.65 times more likely to be forested than pre-settlement condition. Conversely, the pre-settlement condition was more likely to be open than current conditions.

Table 2
The percent of quadrats ($n = 2000$) with or without forest cover, and mean opening and forest canopy patch lengths prior to settlement and currently (One standard error in parentheses).

	Pre-settlement			Current		
	Percent of quadrats (%)	Mean patch length (m)	Number of patches	Percent of quadrats (%)	Mean patch length (m)	Number of patches
Forest canopy	57.4	34.6 (2.7)*	326	83.1	118.2 (15.4)*	138
Opening	42.6	25.7 (1.9)*	325	16.9	26.7 (4.0)*	124

* Statistically significant differences among pre-settlement and current lengths.

Table 3
Mean topographic curvature, slope and elevation of quadrats ($n = 2000$) with and without forest cover prior to settlement and currently. The standard deviation is in parentheses. Also, percent of pre-settlement and current distribution of quadrats with and without forest cover across the four aspects (North, East, South, West).

	Pre-settlement							Current						
	Curvature	Elevation (m)	Slope (%)	Aspect				Curvature	Elevation (m)	Slope (%)	Aspect			
				N	E	S	W				N	E	S	W
Forest	0.0004 (1.2410)	2605.8 (144.0)	21.0 (14.0)	67.2	50.3	48.3	64.4	−0.0778 (1.2528)	2608.0 (153.9)	20.7 (13.7)	88.6	81.1	73.0	91.9
Opening	−0.1868 (1.1223)	2560.5 (165.3)	16.3 (12.4)	32.8	49.7	51.7	35.6	0.0881 (0.8552)	2480.3 (111.0)	10.9 (8.8)	11.4	18.9	27.0	8.1

Prior to settlement, topographic curvature was statistically predictive ($P = 0.002$), with openings associated with negative curvature i.e. upwardly concave (Table 3). When broken down into planform and profile curvature, only planform curvature was significant ($P = 0.029$, profile curvature $P = 0.14$). Aspect was also significantly predictive ($P < 0.001$), with openings more prevalent on S, E, N and W aspects, respectively (Table 3). Slope and elevation were also statistically predictive (both $P < 0.001$) with forest cover associated with steeper slopes and higher elevations. However, site was also statistically significant ($P < 0.001$), suggesting that these topographic gradients do not explain the full variation across the landscape and other variables not measured in this study influence the presence of forest cover.

In contrast to pre-settlement, curvature was not predictive of the presence of current forest cover ($P < 0.001$; Table 3). However, aspect was significantly predictive of forest cover ($P < 0.001$), with openings more prevalent on S, E, N, and W aspects respectively (Table 3). Importantly, the percent of quadrats without forest cover was higher on all aspects historically, but the difference between pre-settlement and current forest cover is greatest on E, W, S, and N aspects respectively (Table 3). Slope and elevation were also a significant predictor of forest cover, with forest cover more likely on steep slopes ($P < 0.001$) and at higher elevations ($P < 0.001$; Table 3). Consistent with pre-settlement trends, significant variation remained between sites ($P < 0.001$).

Pre-settlement opening size and forest patch length did not differ among sites ($P = 0.39$ and 0.92 respectively). However, current opening length and forest patch length were different among sites ($P = 0.17$ and $P = 0.0036$, respectively).

In terms of forest patches, there was a statistically significant difference between pre-settlement and current patch length ($P < 0.001$), with current forested patches approximately 3 times longer on average currently than prior to settlement (34.57 m long prior to settlement compared to 118.18 m currently; Table 2).

In addition, there was a 1 m increase in opening length between pre-settlement and current conditions (Table 2). While this statistically significant ($P = 0.024$), the difference between the means is small. While site was retained in the model as a random factor in both of these analyses, it was not statistically significant in either model ($P = 0.61$ and 0.065, respectively).

Both the forest patch and opening size distributions differ significantly today from prior to settlement ($P < 0.001$ and $P = 0.046$, respectively; Fig. 3). The fitted negative power functions were all statistically significant (Fig. 3 and Table 4, all regression p-values <0.001), with large coefficients of determination (all $R^2 > 0.75$, Table 4) suggesting that the negative power function was a good fit for the data. The y-intercept was only statistically significant for the current size distribution of forest patches ($P = 0.0067$, all other p-values >0.1; Table 4). The slope coefficient was highly significant for all four size frequency distributions (pre-settlement and current forest patch and opening size distributions) with p-values less than 0.001 (Table 4). The slope coefficient prior to settlement for both forest patches and openings was significantly larger than currently (all $P < 0.001$), suggesting that the slope of the curve was steeper and there were proportionally more small openings historically (Table 4).

4. Discussion

The results of this study suggest that both the overall abundance of forest cover and the average forest patch length of Front Range's montane ponderosa forest cover have significantly increased since pre-settlement conditions. Mean forest cover increased from 57% to 83% (conversely openings fell from 43% to 17%), while the mean forest patch length increased from 35 to 118 m long. However, the mean patch length of openings has changed little, increasing 1 m from 26 to 27 m long. Furthermore, while the of forest patch and opening lengths followed a "reverse-J" shaped distribution consistent with our hypotheses and a number of other published studies (Fry et al., 2014; Lydersen et al., 2013; Halofsky et al., 2011; Perry et al., 2011; Collins and Stephens, 2010; Stephens and Fry, 2005; Piirto and Rogers, 2002;Johnson et al., 1998; Skinner, 1995) both prior to settlement and currently; the distribution of both the forest patch and opening lengths has changed over time. Forest patches and openings exhibit shallower decay curves currently than pre-settlement, with proportionally fewer small patch lengths (<50 m long). This suggests that changes in forest management after settlement and the subsequent forest regeneration have filled-in forest openings as hypothesized and reduced the abundance of openings. However, there has been predominantly a loss of small openings rather than large ones, contrary to our hypotheses.

Similar to the size of openings prior to settlement in the current study, Stephens and Fry (2005) also found that openings in a sugar

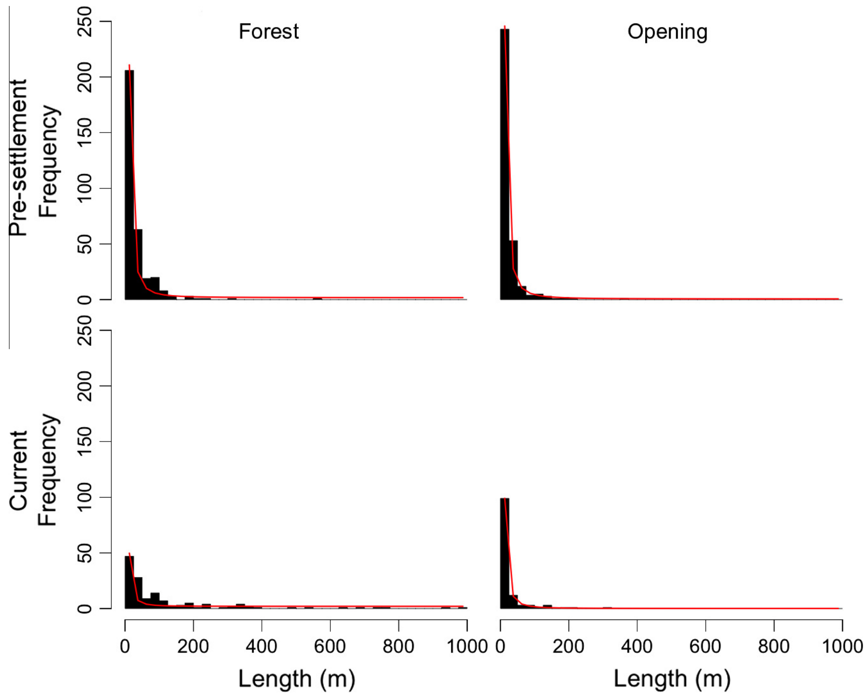

Fig. 3. Size frequency distributions of forest patch and opening lengths prior to settlement and currently (black bars. Frequency (*y*-axis) in terms of the total number of openings or patches, and length of patch or opening (*x*-axis) in meters. Negative power functions (in red) were fitted using linear regression (see Table 4 for coefficients and *p*-values). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 4
Coefficients, *p*-values and R^2 values of negative power functions fitted to the forest patch and opening length frequency distributions using linear regression.

	Forest		Opening	
	Pre-settlement	Current	Pre-settlement	Current
n (Number of patches)	326	138	325	124
b_0 (Intercept)	1.7	1.9	0.6	0.06
Intercept *P*-value	0.13	0.007	0.38	0.46
b_1 (Slope)	32674.5	7467.9	38315.7	15473.8
Coefficient *P*-value	<0.001	<0.001	<0.001	<0.001
Overall regression *P*-value	<0.001	<0.001	<0.001	<0.001
R^2	0.96	0.76	0.99	0.99

pine (*Pinus lambertiana*)-mixed conifer forest in northwestern Mexico with an intact fire regime were generally small (<100 m^2). However, the maximum opening size found by Stephens and Fry (2005) was just 674.8 m^2. In addition, these openings accounted for only 3.8% of the total study area, compared to 42.6% prior to settlement in the current study. It is difficult to directly compare the area metrics used in their study to the transect lengths in the current study because forest openings are irregularly shaped (Lydersen et al., 2013; Skinner, 1995 and the transect lengths used in the current study cannot be directly converted to an areal measurement. However, these results suggest that openings in the sugar pine-mixed conifer forest are rarer and may be somewhat smaller than those detected prior to settlement in montane ponderosa pine on the Front Range. These differences in patch size may also be explained by differences in the fire regime, with the sugar pine-mixed conifer forest experiencing more frequent, lower severity fires (Agee, 1998).

The small increase of mean opening length was unexpected, but is logical given the loss of small openings since the pre-settlement era but relative stability of large opening abundance as demonstrated by the size frequency distributions. Small openings are more likely to be completely filled-in by regenerating trees than large openings in the absence of natural fire regimes due to the large edge to interior area ratio of these openings and the shorter dispersal distances needed for seed to reach the center of a small opening (Greene and Johnson, 1996; Clark et al., 1999). Similarly, small openings are more likely to have abiotic environments that are more amenable to regeneration as the edges of the surrounding canopy moderates the abiotic extremes (Bonnet et al., 2005). It was also expected that large openings would be reduced in size by the regeneration of trees near the edges of the opening for the same reasons. However, the persistence of these large openings suggests that the abiotic environment of these large openings is different from that of the small openings, and is preventing forest invasion despite the lack of fire due to anthropogenic fire suppression. For example, they may be prone to extended periods of saturated soils (e.g. ephemeral wetlands), or have poor soils (e.g. very dry, infertile or shallow soils), or cold air drainage (Coop and Givnish, 2007, 2008) that prevents the establishment of tree regeneration.

Lydersen et al. (2013) also found a loss of openings over time in the mixed conifer forests of the central Sierra Mountains. In 1929, prior to logging, openings at their study site ranged from 112 m^2 (the minimum opening size) to greater than 1000 m^2, with 35.3 openings per hectare. However, by 2007 there were just 0.4 openings per hectare with all openings less than 250 m^2. However, the study design was focused on finer scale spatial patterns rather than larger landscape scale patterns of forest, and does not provide information about openings larger than the plot (4 ha). The loss of these openings in the central Sierra Mountains mirrors the loss of small openings (<50 m long) in the current study.

In contrast with our results, Skinner (1995) found a loss of large openings over time; however, direct comparisons between these studies are complicated by variations in study design and forest types. Skinner (1995) found that mean opening size measured using aerial imagery in the Douglas-fir-hardwood forests of California's Klamath Mountains declined by half from 0.53 ha to 0.27 ha, and the maximum opening size declined by from 297.8 ha to just 54.6 ha between 1944 and today. The differences among these studies may be attributed to variation in the methods, the metrics used, and the definition of a forest patch. Furthermore, the forest composition of the two studies differs, with the Klamath Mountains being dominated by Douglas-fir-hardwood forests (as opposed to ponderosa pine) with historically low severity fire regimes. Variations in forest composition and historical fire regime are likely to influence differences among the pattern of forests across the landscape.

The findings of the current study indicate that forest managers restoring montane ponderosa forests on Colorado's Front Range should increase the abundance of openings through silvicultural treatments, focusing particularly on increasing the abundance of small openings (<50 m long) by breaking down large contiguous forest patches (<50 m long) into smaller patches (<50 m long). While openings should be created on all aspects, they should be predominantly concentrated on the South- and East- facing slopes, with greater abundance of forest patches on North and West aspects. Furthermore, in the absence of the natural mixed-severity fire regime to maintain these forest structures, forest managers should plan periodic maintenance treatments that reduce the prevalence of regeneration but allow for the creation of some new openings and regeneration of others within a dynamic shifting mosaic.

The sample design of 20 transects clustered at four sites used in this study is unlikely to detect rare events; therefore, it is possible that larger openings analogous to those created by modern large severe wildfires may have been present in the landscape historically but not detected by this study. However, this shortcoming would not alter the implications for montane ponderosa forest restoration. Our recommended focus on recreating small openings would still stand if infrequent but very large openings occurred on the Front Range as a result of the mixed-severity fire regime. High-severity fire during periods of unusually hot, dry and windy weather that results in very large openings would have occurred from time to time as part of a mixed-severity fire regime. While modern fire suppression is effective at reducing the occurrence of low and moderate severity fires, these high-severity fires continue to occur. Therefore, very large openings (>100 ha) are still being created by wildfire despite our best efforts to suppress them and additional very large openings do not need to be created through forest restoration treatments.

Similar to all studies that use modern evidence to reconstruct historical forest composition or structure, this study is limited in that the ''absence of evidence is not evidence of absence''. Specifically, the lack of evidence of historical forest cover does not necessarily preclude the presence of forest cover historically. The evidence of historical forest cover may not be present because it has been disturbed or decomposed. However, productivity and decay rates are likely to be slow in the montane forests of Colorado's Front Range due to the relatively dry climate (Harmon et al., 1986) and it is unlikely that all evidence of historical canopy cover would have decomposed over the 150 years since settlement. In addition, since settlement the natural fire disturbance regime that would normally ''decompose'' historical evidence of forest cover has been absent. Furthermore, the absence of recent disturbances such as forest thinning and wildfire that would disturb or remove evidence of historical forest structure was one of the criteria used to select the sites in this study. Finally, ponderosa pine are known to have a long life span (Huckaby et al., 2003) and live trees older than 150 years are not exceptional on Colorado's Front Range. Therefore, it is likely that evidence of historical canopy cover in 1860 is still present today.

While neither opening nor forest patch length were statistically different among sites prior to settlement, current forest patch length did vary among sites. This suggests that the landscape configuration of these forests has not changed uniformly across the Front Range. Therefore, forest managers must carefully consider their specific site characteristics and context when prescribing forest restoration treatments. Further studies of the historical and current landscape configuration of montane ponderosa forests on Colorado's Front Range are needed to refine our findings and provide further guidance for restoration treatments. First, it would be advantageous to quantify the variation of opening and forest patch sizes across a range of topographic settings (for example, high versus low elevations; north versus south facing slopes; and ridges versus valley draws). It is likely that these topographic features influenced historic fire-severity patterns, and the resulting forest patterns in these forests with mixed-severity fire regimes (Cansler and McKenzie, 2014; Halofsky et al., 2011). In addition, studies investigating the patch geometry historically would also be invaluable to forest managers as they plan restoration treatments. While Skinner (1995) found no difference between historical and current opening shape in the Klamath mountains, it is generally understood that patch shapes with high perimeter to area ratios may have greater influence on ecological processes (such as wildfire behavior and wildlife habitat) than their total area indicates due to the prevalence of edges (Fletcher et al., 2007; Turner, 2001; Finney, 2001). Patches with high edge to interior ratios may act as corridors or as barriers, increasing or reducing landscape connectivity respectively (Ries et al., 2004; Agee, 1998). Therefore, the shape of forest patches and openings created may strongly influence the ecological outcomes of restoration treatments.

While it is likely that the landscape-scale patterns will vary among dry forest ecosystems, the results of this study may be used to generally inform the restoration of other historically mixed fire severity ecosystems. Particularly, while the mean and range of opening and forest patch sizes will differ among ecosystems, the results of this study corroborate the ''reverse-J'' size distribution of openings and forest patches described by others (Collins and Stephens, 2010; Halofsky et al., 2011; Johnson et al., 1998; Perry et al., 2011; Piirto and Rogers, 2002; Skinner, 1995; Stephens and Fry, 2005), with many small openings or patches and relatively few large ones that cumulatively occupy a large portion of the landscape. Therefore, forest restoration in ecosystems with a historically mixed-severity fire regime should aim to re-create this ''reverse-J'' distribution.

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