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Variable Forest Structure and Fire Reconstructed Across Historical Ponderosa Pine and Mixed Conifer Landscapes of the San Juan Mountains, Colorado

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Abstract: Late-1800s land surveys were used to reconstruct historical forest structure and fire over more than 235,000 ha in ponderosa pine and mixed conifer landscapes of the San Juan Mountains, Colorado, to further understand differences among regional mountain ranges and help guide landscape-scale restoration and management. Historically, fire-resistant ponderosa pine forests with low tree density and relatively frequent fire, the most restorable forests, covered only the lower 15%–24% of the study area. The other 76%–85% had dominance by mixed- to high-severity fires. Both ponderosa pine and dry mixed conifer had generally pervasive, often dense understory shrubs, and ~20% of pine and ~50%–75% of mixed conifer forests also had high historical tree density. Intensive fuel reduction and mechanical restoration are infeasible and likely ineffective in the upper part of the pine zones and in mixed conifer, where restoring historical fire and creating fire-adapted communities and infrastructure may be the only viable option. Old-growth forests can be actively restored in the lower 15%–24% of the montane, likely increasing landscape resistance and resilience to fire, but mixed- to high-severity fires did also occur near these areas. This imperfect resistance suggests that fire-adapted human communities and infrastructure are needed throughout the study area.

Keywords: fire; ponderosa pine; mixed conifer; San Juan Mountains; Colorado; land surveys; reconstruction; historical forests; ecological restoration; fire-adapted human communities

1. Introduction

Landscape-scale reconstructions over the last decade have revealed more severe historical fires and more variability in forest structure than previously known in ponderosa pine and mixed conifer landscapes ("montane landscapes" hereafter) of the western USA [1,2], but unexplained differences were found among some nearby mountain ranges [3]. We speculated that the region from northern Arizona to Colorado could be a tension zone in which infrequent episodes of large, severe fires could rapidly transform landscapes that previously had mostly low-severity fire for extended periods, potentially leaving adjoining mountain ranges in different states [3]. Here, I further explore this question with evidence from another mountain range in this area and consider the implications of this new evidence for landscape-scale restoration and management.

Early tree-ring and fire-scar research in northern Arizona found that low- to moderate-severity fire regimes generally fostered open, low-density montane forests, which were historically resistant to severe fires, but were later disrupted by fire suppression, logging, and livestock grazing, which are thought to have led to uncharacteristically severe fires [4]. However, subsequent, larger landscape-scale studies began to show that historical montane landscapes were more variable, with open to dense and young to old forest areas from a mixture of fire severities [1,5,6].

Now, reconstructions over large land areas (41,214 to 405,214 ha), using General Land Office (GLO) surveys, cover >2 million ha of dry forests (ponderosa pine and dry mixed conifer, but not moist mixed conifer forests) in the western USA. All reveal considerable variability in historical forest structure and fire severity, including mixed-(moderate) and high-severity fires [3]. Relatively consistent regional differences in historical fire regimes were found, but with some unresolved inconsistencies [3]. Dry forests in Oregon and California had high median tree densities (191–229 trees/ha for trees ≥10 cm) and dominance by mixed-severity fires. In contrast, dry forests over large areas in northern Arizona had low median tree densities (121–124 trees/ha) and dominance by low-severity fires. However, dry forests on adjacent Black Mesa, Arizona, and in two parts of Colorado had moderate median tree densities (137–183 trees/ha) and yet dominance by high-severity fire. This was the basis of the speculation that the region from northern Arizona to Colorado could be a tension zone. This is a hypothesis Hessburg et al. [6] first suggested may be characteristic of a large mixed conifer landscape, in the Pacific Northwest, studied with early aerial photography.

The purpose here is to further analyze this potential tension zone in a new study area, in the San Juan Mountains of southwestern Colorado, which lies between previous study areas in Arizona and Colorado. Historical montane landscapes are poorly known here, with mostly small focused study areas that provide valuable evidence, but an insufficient basis for understanding this potential tension zone or for guiding landscape-scale restoration and management. One recent landscape-scale study in this area, using early forest atlases (1908–1909) and records, did find substantial mixed- to high-severity fire from 1850–1909 with estimated fire rotations of 133–185 years [7]. This study was coarse in resolution and from 1908–1909 data. More detailed GLO data from decades earlier may further clarify the tension zone and revisit the findings from forest atlas data, while improving the foundation for landscape restoration and management.

2. Materials and Methods

2.1. Overview of Methods

I obtained digital scans of land survey field notes and processed them by manually extracting information and entering it into a geodatabase in ArcGIS 10.6 (Geographical Information System software; ESRI, Redlands, CA), while checking for possible fraud. The study area was refined to remove areas affected by land uses at the time of the surveys. Section-line data, recording dominant trees and shrubs along the line, were used to define vegetation zones for analysis, to provide information about understory shrubs and small trees, and to identify non-forest vegetation that may indicate past mixed- to high-severity fire. Section-corner data, recording bearing-tree information, were used with previously developed algorithms and methods to reconstruct tree density, basal area, quadratic mean diameter, tree species composition, tree diameter distributions, fire severity, fire rotation, and old-growth forests [1]. These reconstructions were cross-validated with data from independent sources (e.g., forest atlas data, early records).

2.2. Study Area, Land Survey Data, Zones, and Affected Areas

Original land surveys were completed by government surveyors in the late-1800s following formal instructions [8]. Surveyors laid out ~9.6 × 9.6 km township borders, then subdivided townships into section lines on all sides of 36 sections, each ~1.6 km × 1.6 km. Section corners were marked at the beginning and end of each ~1.6 km section line and quarter corners at the ~0.8 km halfway mark along the section line.

The initial study area in montane forests in the southwestern San Juan Mountains of Colorado (Figure 1) included section-line data over 773,366 ha in parts of 142 land survey townships. However, many surveys in this area had poor corner data (i.e., all required trees at corners seldom recorded), necessitating a smaller section-corner study area over 279,101 ha (Figure 1, Table 1).

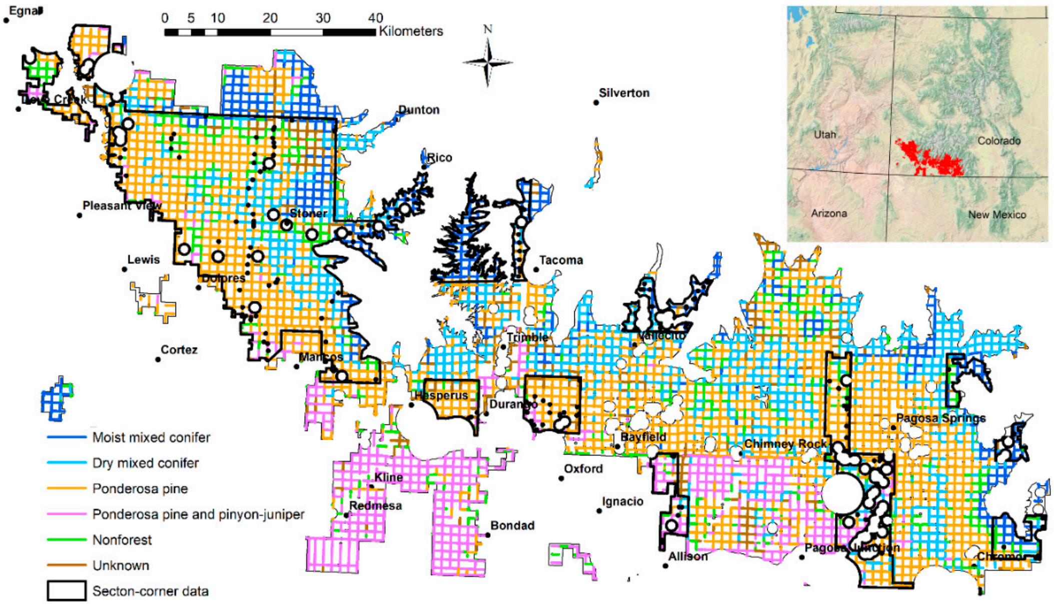

Figure 1. The study area and the historical vegetation zones. See p. 5 for explanations of zones.

Table 1. Initial and unaffected analysis areas by historical vegetation zone, based on section-line and section-corner data.

Historical Vegetation Zone	Lines (km)	Est. Area in Lines (ha)[1]	Lines (%)	Est. Area in Corners (ha)	Corners (%)
Initial analysis area	10,002	773,366		279,101	
Removed affected area[2]	−1580	−106,450		−43,217	
Total unaffected area	8422	666,916		235,884	
Removed-not in a zone[3]	−350	−27,716		−97	
Net unaffected area analyzed	8072	639,200	100.0	235,787	100.0
1. Pine and piñon-juniper	1071	84,809	13.3	13,192	5.6
2. Pine	3215	254,575	39.8	104,059	44.1
3. Dry mixed conifer	1798	142,350	22.3	46,522	19.7
4. Moist mixed conifer	956	75,669	11.8	38,823	16.5
5. Non-forest[4]	532	42,127	6.6	18,998	8.1
6. Unknown[5]	501	39,669	6.2	14,192	6.0

[1] These are estimated from the ratio of analysis area/line length in the total unaffected area. These estimates are possible, because fraction of section-line length is a valid line-intercept estimator of the area of an attribute in the landscape [9]. [2] See Table 2. [3] Not in a zone includes alpine, human-affected lines, lakes, piñon-juniper woodlands, riparian/wetlands, and rock outcrops. [4] Non-forest vegetation was assigned to the corresponding zone where possible, and thus the reported non-forest area is the only part of non-forest that could not be associated with a forest zone. [5] Unknown includes some aspen forests and unidentified forests, along with lines with vegetation not recorded and lines not surveyed.

Field notes were obtained from the Bureau of Land Management, Denver, Colorado. Data were extracted and entered in a geodatabase in ArcGIS 10.6 (ESRI, Inc., Redlands, CA, USA). Digital section lines (CadNSDI PLSS) were from the U.S. Bureau of Land Management [10]. Median survey year across section lines was 1881, and ~88% was surveyed by 1887 (Figure 2).

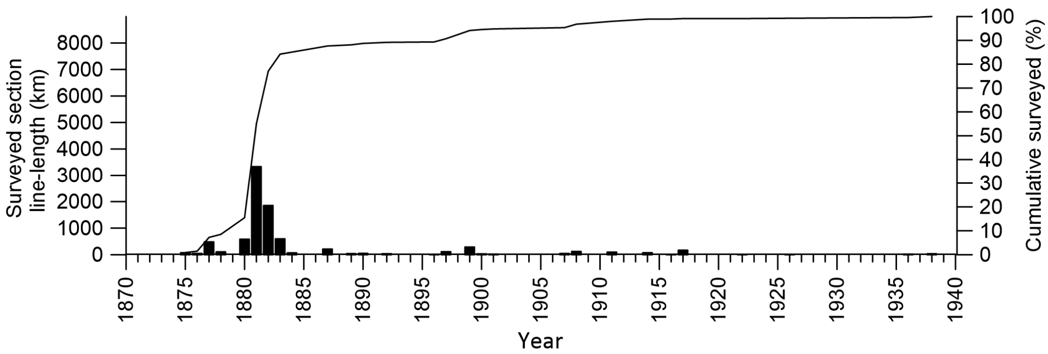

Figure 2. Surveyed section-line length (y-axis) and cumulative percent surveyed for the whole study area. The median survey year was 1881.

Because a GLO fraud syndicate was active in parts of the western USA by 1880 [11], I checked all surveys for fraud. I compared locations of physical features on the plat map with modern topographic maps; fraudulent plats often have obviously mis-mapped physical features. As I entered data into ArcGIS, I periodically measured from distinct recorded physical features (e.g., streams) to these same features on backdrop 1:24,000 scale topographic maps. Some error is in the topographic maps. I found no fraudulent surveys, but I did find some large mapping errors. Most surveyors made some large errors, particularly in difficult terrain (e.g., canyons). A few surveyors made many large errors. I flagged mapping errors ≥140 m. Users can omit these in overlays with other maps, to avoid these errors. After omitting flagged errors, for a sample of the 25 of 39 surveyors, townships had a median of 40.0 m and a standard deviation of 27.7 m in spatial error (Figure 3). This is fairly low error given the optical surveying technology of the late-1800s.

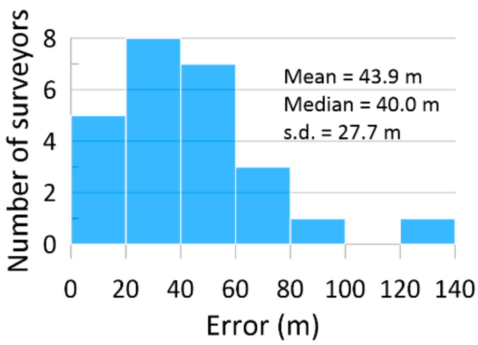

Figure 3. Error in surveyor measurements after removing large errors (>140 m). Data for each surveyor are the means for multiple measurements (usually >10) for each of the 25 of 39 surveyors. Means for each of the 25 surveyors are in Table S4.

Land surveys have often been used in the USA to reconstruct historical vegetation [8]. Surveyors had to record canopy trees in order of abundance on each line and data for bearing trees at corners. I used these to classify forests into zones. Surveyors seldom distinguished Douglas-fir (*Pseudotsuga menziesii*), blue spruce (*Picea pungens*), or Engelmann spruce (*Picea engelmannii*), calling all "spruce" (Table S1). Surveyors recorded just "pine" in ponderosa pine (*Pinus ponderosa*) forests, which likely had some limber pine (*Pinus flexilis*) or southwestern white pine (*Pinus strobiformis*). Junipers (*Juniperus osteosperma, Juniperus scopulorum)* were called "cedar" or "juniper" (Table S1). Twoneedle piñon (*Pinus edulis*) was called pinon. This is a short pine, likely not called pine because it is so small.

I defined four historical montane forest zones (Figure 1, Table 1), generally congruent with modern usage [12]. Pine forests (likely mostly ponderosa pine) were defined by lines with pine alone, but could have small amounts of other tree species, including some juniper (likely mostly *Juniperus scopulorum*). A low-elevation pine and piñon-juniper zone was distinguished by lines with pine and pinon, typically also with junipers (mostly *Juniperus osteosperma*, but some *Juniperus scopulorum*); this zone appeared geographically distinct, not usually spatially intermingled with higher elevation, purer pine forests (Figure 1). Dry mixed conifer forests had pine first (about 75% of lines) or second (about 25% of lines), but with other conifers (blue spruce, Douglas-fir, white fir-*Abies concolor*), and/or quaking aspen (*Populus tremuloides*). Moist mixed conifer had the same trees, sometimes also a few subalpine trees (e.g., Engelmann spruce), but little or no pine (listed in ≥3rd position or not listed).

Section-line segments that were non-forested, not surveyed, or where vegetation was not recorded were placed into the nearest forest zone to enable the zone map (Figure 1) to be as spatially comprehensive as possible and to facilitate analyses by zone. I placed these line segments into the nearest forest zone if all adjacent segments or lines were in this zone, and if elevation and aspect were similar when viewing backdrop US Geological Survey topographic maps while going through unknown line segments. Segments with >1 adjacent zone were left as non-forest, which was the fifth historical zone. These were common where zones nearly met or were interspersed. An Unknown category was used for other segments. I removed line segments in lakes, riparian or wetland areas, identified as rock outcrops, or that represented human land uses (e.g., farm fields).

Limits of the montane were also needed. The lower limit was defined where sagebrush (*Artemisia* spp.) and piñon-juniper without pine became dominant. The upper limit was defined where subalpine forest trees (e.g., subalpine fir-*Abies lasiocarpa*, and Engelmann spruce) became dominant. This upper limit could not be defined by section-line data, since spruce were not distinguished by surveyors. Thus, I identified trees and recorded the GPS elevation of the upper montane limit as I traversed: (1) the southerly-(2925 m) and northerly-facing (2760 m) montane limits on Wolf Creek Pass in the eastern part of the study area, (2) the southerly-facing limit on Coalbank Pass (2900 m) and northerly-facing limit on Red Mountain Pass (2880 m) in the central part of the study area, and (3) the southerly-(2835 m) and northerly-facing (2740 m) limits on Lizard Head Pass in the western part of the study area. Then, I used these as a guide to digitize an approximate upper limit to the montane across the study area. The resulting zone map, thus, approximates historical montane upland forested and non-forested vegetation (Figure 1, Table 1).

Indians were relatively few historically in the study area, and their impacts on the historical fire regime, even after EuroAmerican contact and acquiring horses, were likely limited, concentrated along travel corridors and in other commonly used areas [13]. Their limited effects are considered part of the historical fire regime. Explorers and colonists with horses and mules traveled the Santa Fe Trail south of the San Juan Mountains (Figure 1) in the early 1800s, fur trappers were active by the 1830s, and mining began in the 1870s [14]. The western part was likely grazed by sheep from New Mexico by 1833, but cattle arrived in the 1870s and expanded by the 1880s [14]. In 1903, about 12,000–20,000 cattle grazed the western part of the current National Forest and 268,000 sheep the eastern part [15,16]. Still, many townships recorded good grazing or abundant grass and few settlers at the time of the surveys (Table S2). Logging likely began with mining in the 1870s [16]. Extensive commercial logging likely did not begin until railroad logging in the 1890s near Pagosa Springs [17] and north of Dolores after 1924 [14], although by 1905 six sawmills were operating [18]. Most of the study area was surveyed (Figure 2) before commercial logging and extensive livestock expansion, thus this was a relatively unaltered landscape about to change. The land survey data, although from only a single time period and with some other limitations (Text S1) provide one of the best estimates of the relatively unaltered "historical" forest landscape typically used to guide ecological restoration [8].

In GIS, I buffered land-use locations and removed buffers to focus on relatively unaffected areas. Surveyors recorded locations along or near section lines, when they found land uses (Table 2). They recorded entry and exit locations for larger uses and points for smaller uses. The buffer radii I used (Table 2) approximate an effect zone within which vegetation may have been modified by the land use. The buffer radii were studied in detail in the western Sierra [19]; I analyzed whether the area within varying buffer radii had an elevated abundance of non-forest vegetation indicating clearing or burning. Since lines do not necessarily intersect all land-uses, I erred here toward large buffers.

I combined buffers, then erased affected areas, which were 106,450 ha (13.8%) of the original 773,366 ha total section-line area and 43,217 ha (15.5%) of the 279,101 ha section-corner study area (Table 1). I refer to the remaining ~85% as "unaffected," but buffers are approximations and some land-uses were not fixed in location and could not be fully removed. Total unaffected area was 666,916 ha for section-line data and 235,884 ha for section-corner data (Table 1).

Table 2. Buffer radius and number of land uses recorded by surveyors.

Land Use	Buffer Radius (m)	Number
Building	1000	86
Campground	1000	0
Corral	1000	8
Ditch	100	26
Farm/field	1000	46
Fence	1000	118
Logging	4000	9
Mining	1000	1
Pasture	1000	0
Power line	100	0
Railroad	3220	46
Ranch	1000	2
Reservoir	100	0
Road	200	585
Stock tank	1000	0
Town	1000	2
Trail	200	304
TOTAL NO.		1233
TOTAL LINE LAND-USE AREA (ha)		106,450
TOTAL CORNER LAND-USE AREA (ha)		43,217

2.3. Reconstructing Forest Structure from Section-Line and Section-Corner Data

Surveyors recorded dominant canopy and understory trees and shrubs in order of abundance, using common names (Tables S1 and S3). They were required to record understory shrubs (Table S3), small understory trees (seedlings and saplings <10 cm diameter), and grasses and forbs in order of abundance, using qualitative density terms (e.g., dense, scattered) for shrubs and small trees. Not all surveyors did (Table S4). Few forbs were recorded, and often just "grass." In analyzing general forest understories (e.g., forest/grass, forest/sagebrush), I used only surveyors rated fair or better at understory shrubs (Table S4) and who recorded understory grass at least once. For detailed understories, I used only surveyors who recorded understory trees on at least one line and whose information I rated fair or better for shrubs (Table S4). In analyzing understory tree and shrub density, I included surveyors if they used a density term on at least one section line.

At quarter corners (~0.8 km along a section line), surveyors measured and recorded data for two bearing trees, and at the end (~1.6 km), they recorded data for four trees. For each tree, they recorded species, diameter in inches (2.54 cm) [20], distance in links (~0.2 m), and bearing in degrees. They also recorded some physical features (e.g., streams). An ending township description summarized topography, vegetation, and land-uses (Table S2). Bearing-tree data allow valid reconstruction of tree density, basal area, quadratic mean diameter, composition, diameter distributions, and fire severity [1,20,21]. Surveyors recorded tree data accurately and with little bias [21]. Land survey reconstructions have been critiqued and have some known limitations (Text S1).

I pooled tree data across nearby corners, aiming for a 2:1 ratio of quarter corners to corners in the same zone, to increase accuracy [20]. Six-corner pools (518 ha) were used for tree density, as this pool had lowest relative mean absolute errors (RMAEs = 14%–23%), in accuracy trials in three states [20]. RMAE is absolute error between two variables relative (%) to the variable considered truth, plot data in this case. Similarly, 9 corner pools (777 ha) were used for basal area (RMAEs = 21%–25%), quadratic mean diameter (RMAEs = 12%–16%), and composition, and 12 corner pools for diameters.

I reconstructed tree density using our methods, which estimate the Voronoi area of each bearing tree using regression equations (Table S5) based on estimated crown radius of the tree and mean distance among bearing trees at the same corner [20]. The inverse of mean Voronoi area among trees is tree density, which is for trees generally ≥10 cm diameter-at-stump-height (dsh), about 30 cm [20]. I used the weighted mean-based harmonic Voronoi density (WHVD) estimator, shown to be the only unbiased estimator for both the Mogollon Plateau and the Colorado Front Range, and to have low RMAE of 14%–24% [20]. To calibrate reconstruction equations (Table S5), my assistant and I went to 50 section corners and random sites in relatively undisturbed forests in the study area, on the Uncompahgre Plateau [22], and in the Jemez Mountains, where we repeated a modern survey identical to the original survey. At each point, we measured distance to closest trees in each 90° sector with a laser rangefinder, bearing to the tree with a sighting compass, and tree diameter at 30 cm and at breast height (1.4 m) with a caliper. For each tree, we measured crown radius with a densiometer. To estimate the tree's Voronoi area [23], we measured distance and bearing from the tree's center to the center of ≥5 nearest trees (≥1 tree per 90° sector). I measured the Voronoi area of the tree in ArcGIS. I used 249 trees to develop regression equations for crown radius and Voronoi area (Table S5).

I calculated basal area as the product of mean cross-sectional area of trees in the pool and tree density [20]. I calculated basal area and diameters by converting surveyor measurements of diameter at stump height (DSH; ~30 cm height, [20]) to diameter-at-breast height (DBH; 1.37 m) using regression based on field measurements at the 50 sites (DBH = 1.426 + 0.834 * DSH). I calculated basal area with a PCQ BA estimator in nine-corner pools, which had 21% RMAE in the Colorado Front Range [20]. To reconstruct diameter distributions, using 12 corner pools that were about 87% accurate in the Colorado Front Range [20], I tallied trees in 10 cm bins, congruent with surveyor accuracy. I used a correction for slight under-counting in the smallest size classes [20]. I merged pools across zones for analyzing tree diameters. I relocated bearing trees to resolve uncertain common names (Table S1), and revisited section lines to identify some trees and shrubs (Tables S1 and S3).

2.4. Reconstructing Fire Severity and Old-Growth Forests

As in previous research [19,22], I reconstructed fire severity using modeled and direct evidence from four sources: (1) historical forest structure and (2) historical forest openings, both from bearing-tree data, and (3) historical non-forest and (4) historical scattered timber, both from section-line data. Data in (1) and (2) were converted to lines by intersection with section lines for consistent analysis.

We showed, through calibration with 64 tree-ring reconstructions, that historical forest structure reconstructed from bearing-tree data could be used to accurately model fire severity over the preceding century, and we validated this method with tree-ring reconstructions and independent sources [1,3], including early scientific observations [19,24,25]. Low-severity fire was identified by tree density <177.6 trees/ha for trees ≥10 cm dsh, small conifers (<30 cm) <46.9% and large conifers (≥40 cm) >29.2% of all conifers [1]. High severity was identified by small conifers >50.0% and large conifers <20.0% of conifers. Mixed severity was between these. Reconstruction period is the time for trees to grow to 40 cm [1]. This was 92 years for the San Juans, between 103 years on the Uncompahgre Plateau [26] and 80 years in the Jemez Mountains [27] (p. 24). Reconstructions in moist mixed conifer are preliminary, as calibration was in pine and dry mixed conifer, although tree species are the same.

Openings in forests, lacking bearing trees, may indicate disturbance had removed trees over the distance surveyors searched, typically 300 links or ~60 m from the corner. Often, surveyors recorded "no trees within limits." Where all expected bearing trees at a corner were missing, defined here as an "opening," this area is ≥1.13 ha. As in [19,22], openings were interpreted as high-severity disturbance if canopy density on the line was not recorded (thus likely early- to mid-successional forests). If the forest on the line was mature (e.g., "heavily timbered"), I interpreted openings as likely associated with mixed-severity disturbance.

Historical non-forest that became forested by 2016 was a potential indicator of high-severity fire in forests before the surveys. Non-forest, found on 1372.1 km (17.0%) of 8072.1 km of total section-line length (Table 3, Figure 4), overall was ~52% shrubs, 21% grasslands, 17% dead, fallen, or burned trees, 4% small trees, 3% sagebrush, 2% no timber, and 2% shrubs and small trees (Figure 5, Table 3). Non-forest was only 7%–16% of zones, least in pine and piñon-juniper and most in moist mixed conifer (Table 3). Non-forest was similar in the section-corner area, except non-forest was 13%–20% of zones, and there was less grassland and more dead, fallen, and burned.

Non-forest recorded as: (1) dead, fallen, or burned timber, (2) small trees, or (3) shrubs and small trees likely represents early succession after high-severity forest disturbances. These were either specifically recorded as disturbed or their abundant small trees, particularly fire-stimulated quaking aspen, suggest early recovery after disturbance [12,28–30]. High-severity fires in Rocky Mountain montane forests also historically left behind grasslands and large shrubfields that were slowly re-invaded by trees [31,32]. Surveyors did record some burned forests with non-forest understories of dense shrubs and small trees (Table 4). Non-forest can be permanent in settings unfavorable to forests [31,33]. To distinguish disturbed from more permanent non-forest, in GIS, I intersected historical non-forest with modern forests, from Landfire existing vegetation (Table S6) ca 2016. I considered only non-forest that became forested as potentially created by disturbance, thus a conservative estimate.

Table 3. Historical non-forest in the section-line area and in the section-corner area.

Non-Forest Composition	Overall	Non-Forest Unknown	Pine-PJ	Pine	Dry MC	Moist MC
			Section-line area			
Mixed mt. shrubs (%)	51.8	60.3	55.4	65.6	14.7	26.4
Grasslands (%)	21.2	25.0	9.7	21.7	12.9	22.8
Dead/fallen/burned (%)	16.7	6.5	9.7	7.6	49.9	40.8
Small trees (%)	4.1	0.7	3.0	1.1	18.1	8.1
Sagebrush (%)	3.0	3.9	16.8	1.5	0.3	0.1
No timber (%)	1.6	1.1	4.6	2.2	0.6	1.5
Shrubs and small trees (%)	1.6	2.5	0.7	0.4	3.4	0.3
Total line length (km)	1372.1	531.0	76.9	426.7	187.1	150.4
Percent of zone (%)	17.0	-	7.2	13.3	10.4	15.7
			Section-corner area			
Mixed mt. shrubs (%)	64.4	87.3	69.2	82.3	14.3	18.2
Grasslands (%)	6.4	7.5	16.4	7.7	2.0	3.1
Dead/fallen/burned (%)	21.7	1.0	0.0	7.2	65.0	66.6
Small trees (%)	4.7	1.0	11.0	1.1	14.6	9.7
Sagebrush (%)	0.4	0.4	0.7	0.7	0.0	0.0
No timber (%)	0.5	0.2	0.0	0.7	0.0	1.7
Shrubs and small trees (%)	1.9	2.7	2.7	0.3	4.1	0.7
Total line length (km)	683.7	231.9	21.0	234.2	124.3	72.3
Percent of zone (%)	23.0	-	13.0	18.0	20.2	14.7

PJ = piñon-juniper; MC = mixed conifer.

Scattered timber was abundant, making up ~30%–39% of total forest line length (Figure 4, Table 5). Surveyors often recorded entry/exit locations between mature forests and scattered timber along section lines, and thus scattered timber stood out from mature forests at abrupt boundaries. Scattered timber often had too few bearing trees at corners to enable reconstructions. The area of a circle at the typical

300 link limit surveyors had to search was 1.13 ha. If four trees had been at 301 links, then tree density was ~3.5 trees/ha, but trees were often missing, and so density was likely often <3.5 trees/ha, which would certainly have stood out relative to typical dry forests.

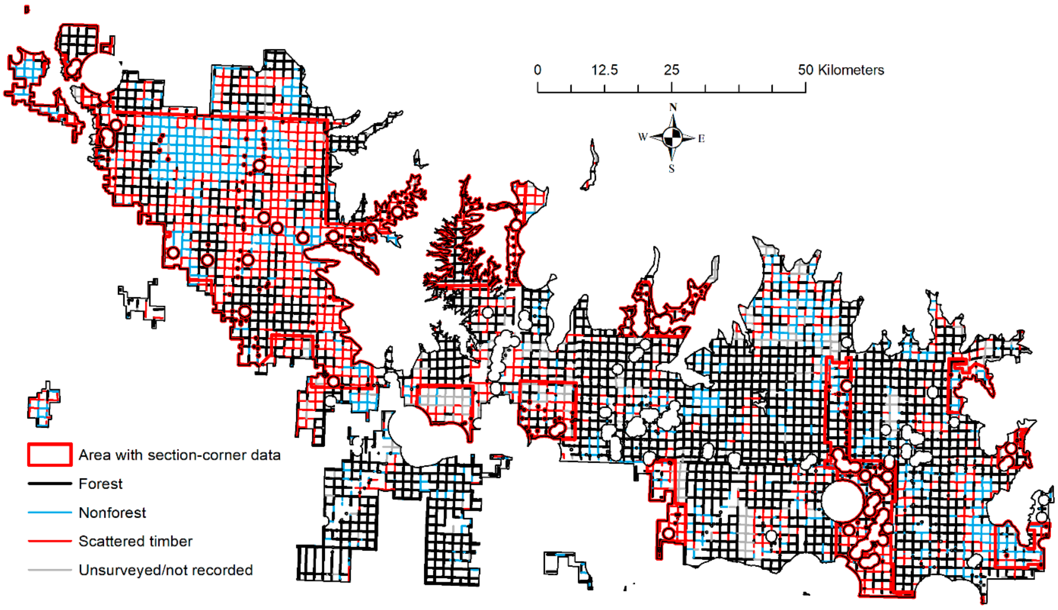

Figure 4. Historical section lines with recorded forest, non-forest, and scattered timber.

Again, to help distinguish disturbed from more permanent scattered timber, I intersected scattered timber with modern Landfire maps of forests (see above). Some modern areas of forest could have remained sparse, but forest typically implies some canopy closure. Scattered timber that did not become forested more likely represents natural, open, very low-density forests in settings that may not physically support denser forest. It is likely that most historical scattered timber that recovered to forest by ca 2016 represents recovery after moderate- to high-severity disturbances, particularly fire, for several reasons. Very low tree density is consistent with tree density expected after high-severity disturbance (≥70% of tree basal area killed [34]), and modern moderate- to high-severity fires can leave scattered surviving trees. Scattered timber recorded in the Sierra Nevada was validated as 80% high-severity fire by mapping done 9–42 years later in 1902 by Leiberg [19]. On the Uncompahgre Plateau north of this study area, three 1903 photographs show scattered timber from fire in dry forests, and two fire-scar dates in scattered timber identify fire as the agent [22]. In this San Juan study area, surveyors directly recorded two cases where fire produced scattered timber (Table 4). Early observations from the study area and nearby areas corroborate that scattered timber, often with small regenerating trees beneath, resulted from high-severity fires (Table S7: Q1, Q3, Q6–Q9). Some could have been from other disturbances (e.g., severe droughts, bark-beetle outbreaks), but fire is the likely explanation for most scattered timber that recovered to forest. However, the moderate- and high-severity parts cannot be distinguished. To roughly estimate fire rotations, I assumed scattered timber represents half mixed-and half high-severity fire.

Fire was also distinguished from other disturbances by spatial contiguity suggesting fire spread, apparent directional spread, sharp boundaries with mature, unburned vegetation, and by early post-fire vegetation (e.g., quaking aspen) known to be stimulated by fire [28–30]. After applying these criteria with the four sources of fire severity information, I combined them to map fire severity and to estimate fire rotation, the expected time to burn once across a landscape [32].

Old-growth forests can be reconstructed from GLO data using recorded tree diameters and estimated tree density, as in [35], which found old growth across 76% of a 280,000 ha historical dry-forest landscape in Oregon. Here, I used a similar method. To estimate historical old growth, I used the old-growth definition for interior ponderosa pine in the Southwest [36] for the pine zone and the mixed-species group in [37] for dry and moist mixed conifer. Mehl [36] specified ≥10 trees/acre ≥18" dbh; I used ≥24.7 trees/ha ≥50 cm dbh, a slightly larger diameter, consistent with diameter-class breaks that are congruent with the precision of surveyor diameter estimates [21]. Popp et al. [37] specified ≥12 trees/acre ≥18" dbh for low sites; low and high sites could not be discriminated in GLO data. I used the low site definition. Thus, ≥29.6 trees/ha ≥50 cm dbh. Other criteria (e.g., dead trees, decadence, etc.) in the definitions cannot be reconstructed from GLO data. I used section-line descriptions (e.g., heavy timber) to further understand old growth on lines.

Table 4. Examples of surveyor direct records of burned timber, scattered timber, recovering post-fire shrubs and aspen, and large, likely old trees.

Moderate- to High-Severity Fires in All Forest Zones
Burned pine and piñon-juniper forests
Covered with burnt, dead, and live timber of Pine Pinon and Cedar ... Scattering grama grass (Tyler & Medary, 1881, T034NR012W) [1]
Burnt pinon, Pine & Cedar (Geo. D. Nickel, 1880, T033N R001W)
Burned pine forests
Some grass; dead and young pines (James M. Boggs, 1883, T037NR003W)
Burnt Pine Timber (Frank W. Gove, 1881, T038NR013W)
Pine and burnt and fallen timber (Gardner & Cleghorn, 1882, T036NR005W)
Burned dry mixed conifer forests
Burnt and fallen timber. Pine and spruce (Gardner & Cleghorn, 1882, T036NR005W)
Burnt Pine. Scattering Aspen & Cottonwood (Frank W. Gove, 1881, T038NR013W)
Dense undergrowth Aspen. Burnt Pine (Frank W. Gove, 1881, T038NR013W)
Burned moist mixed conifer forests
Timber, aspen and spruce. Burnt and fallen timber (Benjamin Smith, 1883, T033N R001E)
Timber Spruce and aspen badly burned and fallen (Edwin H. Kellogg, 1897, T033NR002E)
Scattered Timber from High-Severity Fires
Scattering pine and much burnt and fallen timber (James M. Gardner, 1882, T035NR005W)
Some pine, much fallen timber (James M. Gardner, 1882, T035NR005W)
Burned Forests with Recovering Dense Mixed Mountain Shrubs and/or Aspen
Dead and/or burned timber with a dense understory of Gambel oak (mixed mountain shrubs)
Burnt Pine. Dense undergrowth of Oak brush (Frank W. Gove, 1881, T038NR013W)
Dense undergrowth of oak brush. Burnt Pine, Aspen Groves (Frank W. Gove, 1881, T038NR013W)
Pine timber with dense undergrowth of oak brush also much fallen timber (James M. Gardner, 1882, T035NR005W)
Dead and/or burned timber with dense young aspen
Dense undergrowth Aspen. Burnt Pine (Frank W. Gove, 1881, T038NR013W)
Timber burnt off, followed by a dense undergrowth of aspen (Benjamin H. Smith, 1883, T034NR001)
Fire killed timber, and Aspen brush ... Dead spruce timber (William Cochrane, 1887, T035NR001E)
Potential Old-Growth Forests or Areas of Large Trees
Heavily timbered with large pines, pinons & cedars. Good grass (Tyler & Medary, 1881, T034NR010W-South of the Ute line)
Scattered, heavy pine timber. Dense oak brush (Frank W. Gove, 1880, T038NR015W)
Some very good pine timber (William H. Clark, 1882, T037NR009W)
Lofty pines scattering, no underbrush (William H. Cochrane, 1887, T036NR001W)
2nd half mile Mesa covered with fine large pine timber. Good grass (Henry C. Hopper, 1877, T035NR008W)

Notes: [1] The surveyor's name, the date of the survey, and the township are given in parentheses.

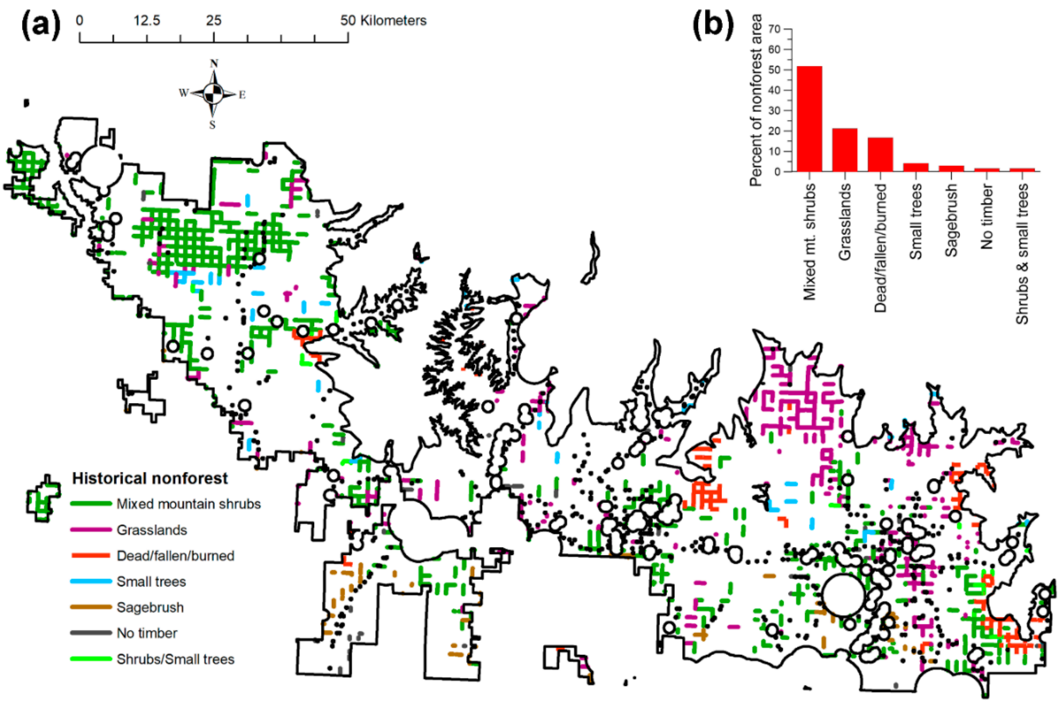

Figure 5. The seven types of non-forest vegetation at the time of the surveys: (**a**) across the study area, and (**b**) their relative extent.

Table 5. Historical section-line length recorded as scattered timber and the succession of scattered timber from the median survey year of 1881 to forest circa 2016 by zone.

	In Section-Line Area			In Section-Corner Area		
Historical Zone	**Km[1]**	**% of Forest in Zone[2]**	**% Now Forested[3]**	**Km[1]**	**% of Forest in Zone[2]**	**% Now Forested[3]**
Pine and piñon-juniper	184.6	18.7	63.4	67.4	41.8	71.0
Pine	846.9	31.7	70.1	451.8	34.8	70.8
Dry mixed conifer	396.6	25.0	76.1	282.9	46.0	75.9
Moist mixed conifer	289.5	37.7	77.0	183.7	37.2	78.5
Unknown	125.4	72.8	64.9	91.7	52.9	66.2
TOTAL SCATTERED	1843.0	29.8	71.3	1077.5	39.3	72.9
TOTAL FOREST	6183.8			2742.1		

[1] Data are the unaffected section-line length recorded as scattered timber, by zone. [2] Data are the percentage of unaffected forested section-line length recorded as scattered timber in historical forests (non-forest omitted), by zone. [3] Data are the percentage of the historical scattered timber that was forested by ca 2016, by zone.

2.5. Cross-Validation

The GLO method already has substantial validation, using large modern accuracy trials and historical cross-validations in several states [3,20]. This validation includes (1) 20 modern validations that replicated the survey method at 499 corners in three states and compared results to data from plots centered over the corner, (2) 47 detailed "specific cross-validations" from overlaying GLO estimates with estimates from independent historical sources, (3) six locations with "general cross-validations" that compared GLO estimates to nearby historical estimates that could not be overlaid, and (4) 99 supporting historical observations and estimates from paleo-reconstructions and early scientific research. In contrast, tree-ring reconstructions have only one major cross-validation at 15 sites [38], which showed tree density is underestimated by ~9%. Similarly, one modern validation shows a spatial fire-history method can estimate fire rotation within ~10% [39].

Here, I further cross-validated locally with a tree-ring reconstruction of tree density and basal area (Tables S8 and S9), with age-structure/charcoal estimates of fire severity (Table S10), and with forest atlases. Corroboration also came from early historical accounts near the study area and the region (Table S7). I did not cross-validate with estimates from stumps [12], as this method is not yet validated. I made specific comparison if I had a GLO reconstruction polygon(s) that covered or was near the site. Otherwise, other studies provided general estimates I compared to overall GLO estimates. I used RMAE as the measure of accuracy. To be used, fire histories had to explicitly reconstruct fire severity using age structure or other methods.

3. Results

3.1. Reconstructed Tree Density, Basal Area, Composition, Diameters from Section-Corner Data

Sample areas for each bearing-tree analysis (e.g., Table 6) cover the available area with tree data, and are equal to or are a little less than the area of available 6 corner (105,696 ha), 9 corner (101,983 ha), and 12 corner pools (104,108 ha). The rest of the section-corner analysis area was largely openings, including non-forest, scattered timber, openings in forests, etc.

Table 6. Variability in reconstructed historical tree density (trees ≥10 cm dsh) in the section-corner area.

Variable	Pine and Piñon-Juniper	Pine	Pine Zones	Dry Mixed Conifer	Dry Forests	Moist Mixed Conifer [1]	Whole Montane
Tree density sample							
Sample polygons (n)	13	80	93	42	135	38	173
Sample area (ha)	7805	46,428	54,233	25,669	79,902	24,734	104,636
Tree density							
Mean (trees/ha)	303	144	166	245	191	435	244
SD (trees/ha)	320	158	194	170	190	566	328
CV (%)	106	110	117	69	99	130	134
Minimum (trees/ha)	56	20	20	35	20	100	20
1st quartile (trees/ha)	135	69	73	95	80	175	89
Median (trees/ha)	209	97	107	200	118	286	150
3rd quartile (trees/ha)	320	150	184	393	236	449	301
Maximum (trees/ha)	1311	1160	1311	672	1311	3493	3493
Percentage (%) of pools by density class							
<100 trees/ha	7.7	52.5	46.2	31.0	41.5	0.0	32.4
100–200 trees/ha	38.5	33.7	34.4	19.0	29.6	34.2	30.6
>200 trees/ha	53.8	13.8	19.4	50.0	28.9	65.8	37.0
>300 trees/ha	23.0	8.8	10.8	35.7	18.5	47.4	24.9

Reconstructed mean historical tree densities in a 104,636 ha analysis area were 191 trees/ha across dry forests and 244 trees/ha across montane forests (Table 6, Figure 6a). Median tree densities were 118 trees/ha across dry forests and 150 trees/ha across montane forests (Table 6). Mean and median tree densities were lowest (144 trees/ha and 97 trees/ha, respectively) in pine, but about twice as dense in pine and piñon-juniper (303 trees/ha and 209 trees/ha) and dry mixed conifer (245 trees/ha and 200 trees/ha). Moist mixed conifer had the greatest mean (435 trees/ha) and median (286 trees/ha) tree densities (Table 6). Open, low-density forests (<100 trees/ha), were most common in pine (53% of pools), less so in dry mixed conifer (31%), rare in pine and piñon-juniper (8%), and absent in moist mixed conifer (Table 6). Low-density forests covered some ≥5000 ha contiguous areas (Figure 6a).

Dense forests (>200 trees/ha) in 29% of dry-forest pools and 37% of the montane, were only 14% of pine, but >50% of dry mixed conifer, moist mixed conifer, and pine and piñon-juniper forests (Table 6). Very dense forests (>300 trees/ha) were found across only 9% of pine, but 23% of pine and piñon-juniper, 36% of dry mixed conifer, 47% of moist mixed conifer, 19% of dry forests, and 25% of the montane, Historical tree density was highly spatially variable, with a CV of 134% across montane pools and 69%–130% across pools in individual zones (Table 6). Maps of historical tree density by zone are in Figures S1–S5.

Mean historical basal areas were reconstructed in a 101,983-ha analysis area to have been 11.7 m^2/ha in dry forests and 11.6 m^2/ha across the montane (Table 7, Figure 6b). Corresponding median basal areas were 10.3 and 10.0 m^2/ha. Variability in basal area, with CVs mostly <50%, appeared lower than for tree density, but may just be from larger pools. Mean (11.2–12.8 m^2/ha) and median (8.4–10.8 m^2/ha) basal areas varied little among forest zones. Low basal area (<8 m^2/ha) was found in 10% of pine and piñon-juniper, 24% of pine, 30% of dry mixed conifer, and 42% of moist mixed conifer. High basal area (>15 m^2/ha) was found in 30% of pine and piñon-juniper, 15% of pine, 30% of dry mixed conifer, and 17% of moist mixed conifer. The largest quartile of basal areas was 18.1–22.6 m^2/ha in pine and piñon-juniper, 13.6–21.7 m^2/ha in pine, 15.2–30.6 m^2/ha in dry mixed conifer, and 14.4–37.6 m^2/ha in moist mixed conifer. QMDs, with CVs of 14%–26%, varied less than basal areas. Mean and median QMDs were 24.9–44.4 cm, highest in pine and lowest in moist mixed conifer (Table 7). Historical basal area by zone is shown in Figures S6–S10. A map of historical QMD across the montane is in Figure S11.

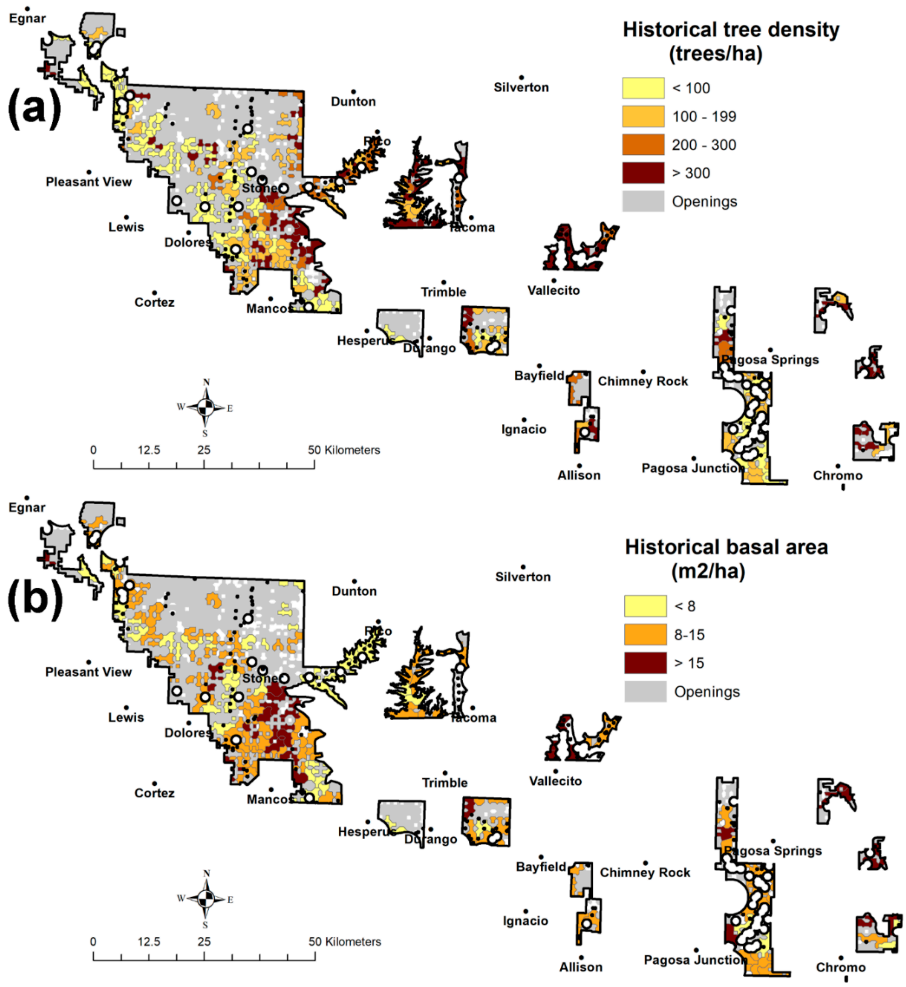

Figure 6. Reconstructed historical (**a**) tree density (trees/ha for trees ≥10 cm dsh) and (**b**) basal area (m^2/ha) across the montane section-corner study area.

Shade-tolerant trees were rare in both pine zones and more common in mixed conifer zones (Table 8). Shade-tolerant trees appeared to increase up valleys and slopes across the study area (Figure 7). In the lowest pine and piñon-juniper zone, piñon and juniper are left out of this comparison, and so shade-intolerant trees have a mean of only 51%. In pine, there were almost no shade-tolerant trees. In dry mixed conifer, only about a quarter of the zone had >4% shade-tolerant trees, but in that quartile, they ranged from 4% to 70% with a mean of 22%. Shade-tolerant trees were 44% of trees in moist mixed conifer. This pattern matches classification; as pine has aspen and some shade-tolerant trees, the dry mixed conifer zone is defined, and as pine declines and shade-tolerant trees and aspen become dominant, the moist mixed conifer zone is defined.

Table 7. Variability in reconstructed historical basal area and quadratic mean diameter in the section-corner area.

Variable	Pine and Piñon-Juniper	Pine	Pine Zones	Dry Mixed Conifer	Dry Forests	Moist Mixed Conifer[1]	Whole Montane
Basal area and quadratic mean diameter sample							
Sample polygons (n)	10	54	64	27	91	24	115
Sample area (ha)	7869	46,063	53,932	24,290	78,222	23,761	101,983
Basal area							
Mean (m^2/ha)	12.8	11.2	11.5	12.2	11.7	11.2	11.6
SD (m^2/ha)	5.5	4.4	4.6	5.9	5.0	8.5	5.8
CV (%)	43.0	39.3	40.0	48.4	42.7	75.9	50.0
Minimum (m^2/ha)	4.3	4.0	4.0	5.3	4.0	2.7	2.7
1st quartile (m^2/ha)	9.4	8.2	8.6	7.6	8.2	5.1	7.6
Median (m^2/ha)	10.8	10.1	10.2	10.4	10.3	8.4	10.0
3rd quartile (m^2/ha)	18.1	13.6	14.1	15.2	14.4	14.4	14.4
Maximum (m^2/ha)	22.6	21.7	22.6	30.6	30.6	37.6	37.6
Percentage (%) of pools by basal-area class							
<8 m^2/ha	10.0	24.1	21.9	29.6	24.2	41.7	27.8
8–15 m^2/ha	60.0	61.1	60.9	40.8	54.9	41.7	52.2
>15 m^2/ha	30.0	14.8	17.2	29.6	20.9	16.6	20.0
Quadratic mean diameter (cm)							
Mean (cm)	32.9	44.4	42.6	35.1	40.4	24.9	37.1
SD (cm)	6.8	6.0	7.4	7.0	8.0	4.2	9.7
CV (%)	20.7	13.5	17.4	19.9	19.8	16.9	26.1
Minimum (cm)	21.2	30.6	21.2	24.5	21.2	17.3	17.3
1st quartile (cm)	27.1	41.3	39.1	28.3	34.2	21.1	28.3
Median (cm)	33.5	44.2	43.0	35.2	41.8	25.3	39.4
3rd quartile (cm)	38.4	47.9	47.4	41.0	45.3	27.0	44.4
Maximum (cm)	43.6	58.0	58.0	46.3	58.0	34.6	58.0

Bearing trees were numerous enough in a 104,108 ha analysis area for diameter distributions by zone (Figure 8). Total trees were 2924. Juniper, piñon, and quaking aspen had inverse J-shaped distributions with most <40 cm. Pine distributions were peaked in the 30–40 cm size class in both pine zones and dry mixed conifer (Figure 8). Small trees (<40 cm dbh) dominated all zones (Figure 8). Trees <40 cm were 70.1% of all trees and 51.3% of pines. In pine and piñon-juniper, most junipers and piñons and 61% of pines were <40 cm dbh. In pine, 53% of trees were <40 cm. In dry mixed conifer, most aspen, shade-tolerant trees, and 41% of pines were <40 cm. In moist mixed conifer, >90% of trees were <40 cm dbh.

However, ecologically significant large pines were prominent in the three dry-forest zones (Figure 8, Table 9). Percentage of large pines of all sizes increased from pine and piñon-juniper to dry mixed conifer, which consistently had the most large trees (Table 9). In the pine zones, almost half of pines were >40 cm, about 1/3 was >50 cm, and about 1/6 was >60 cm. Very large pines (>80 cm) were only 1.3% of pines in the pine zones, but 3.6% in dry mixed conifer. The six largest recorded bearing trees were pines. One was 183 cm just east of Weber Reservoir near Mancos, one was 142 cm, one was 137 cm, three were 122 cm, and two were about 1.6 km north of Weber Reservoir.

Table 8. Historical tree composition, in the section-corner area, that was shade-tolerant (blue spruce, Douglas-fir, and white fir), and shade-intolerant trees (quaking aspen and pine).

	Pine and Piñon-Juniper	**Pine**	**Dry Mixed Conifer**	**Moist Mixed Conifer**
Sample polygons (n)	10	54	27	24
Sample area (ha)	7869	46,063	24290	23761
Shade-tolerant trees (blue spruce, Douglas-fir, white fir)				
Mean (%)	0.76	0.22	5.98	43.71
SD (%)	1.60	0.92	15.13	22.72
Minimum (%)	0.00	0.00	0.00	0.00
1st quartile (%)	0.00	0.00	0.00	27.63
Median (%)	0.00	0.00	0.00	43.21
3rd quartile (%)	0.00	0.00	4.35	61.55
Maximum (%)	4.00	4.17	70.00	86.96
Shade-intolerant trees (pine and quaking aspen)				
Mean (%)	51.39	95.91	91.21	55.14
SD (%)	34.53	6.75	15.44	23.14
Minimum (%)	6.25	73.08	30.00	12.00
1st quartile (%)	21.09	95.18	90.91	38.45
Median (%)	43.32	100.00	96.30	56.00
3rd quartile (%)	88.29	100.00	100.00	72.37
Maximum (%)	100.00	100.00	100.00	100.00

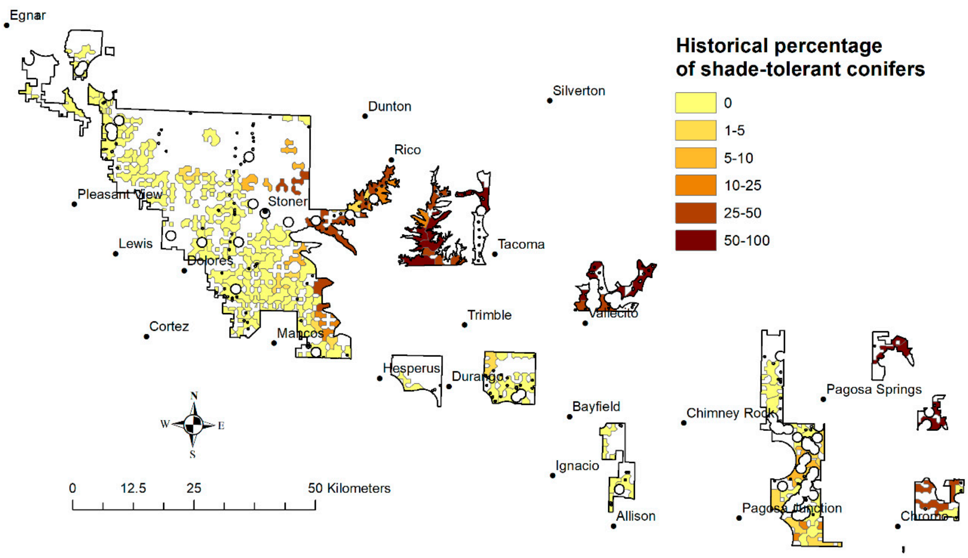

Figure 7. Reconstructed historical composition (%) of shade-tolerant conifers (blue spruce, Douglas-fir, and white fir).

Table 9. Percentage of total pines recorded as bearing trees, in each zone and in the two pine zones together, that exceeded particular diameters.

Diameter (DBH)	Pine and Piñon-Juniper	Pine	Pine Zones	Dry Mixed Conifer
>30 cm (%)	70.2	75.8	75.4	80.3
>40 cm (%)	39.3	46.8	46.2	59.1
>50 cm (%)	17.9	33.1	31.9	41.4
>60 cm (%)	5.3	17.2	16.2	18.1
>70 cm (%)	0.9	4.5	4.2	7.4
>80 cm (%)	0.0	1.4	1.3	3.6
Pines (n)	110	1266	1376	343

3.2. Reconstructed Forest Understories and Their Trees and Shrubs from Section-Line Data

Forest understories varied, with some consistent understories across large areas and other areas having finer mixes (Figure 9). Forest understories were dominated by mixed mountain shrubs in all zones, except possibly in moist mixed conifer (Table 10, Figure 9). Dry mixed conifer had 85% and pine had 83% coverage of understory mixed mountain shrubs. Pine and piñon-juniper, in contrast, had 42% grass, 14% sagebrush, and only 44% mixed mountain shrubs. Moist mixed conifer likely also had less mixed mountain shrubs, possibly just 28%, but understories are uncertain in this zone. Understory trees were present on only 1% of the two pine zones, but on 13%–14% of dry and moist mixed conifer (Table 11). Quaking aspen were almost all the understory trees in all zones. In mixed conifer, understory trees were dense (fraction 0.73 in dry mixed conifer, 0.94 in moist mixed conifer).

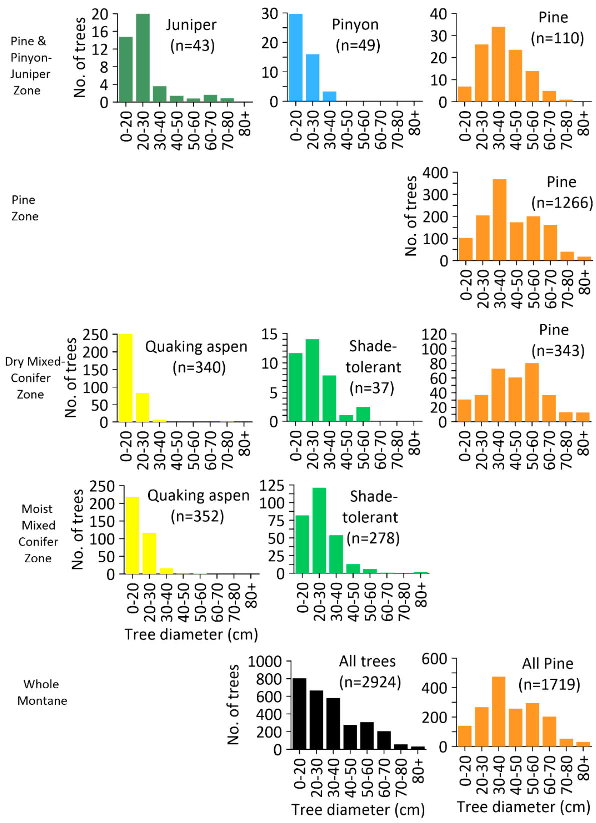

Figure 8. Historical tree diameter distributions (diameter at breast height or dbh; about 1.37 m above the base) by species, including only tree species with >35 trees. Shade-tolerant conifers included blue spruce, Douglas-fir, and white fir.

In the few places they occurred. Mixed-mountain-shrub understories were dominated by Gambel oak, recorded first on 98%–99% of line lengths except in pine and piñon-juniper where it was first on 90% of line length, sagebrush was first on 8.5%, and Utah serviceberry first on 1.5% of line length (Table 11). Shrubs other than Gambel oak were present, but usually on <15% of line length, and often were mostly Utah serviceberry or sagebrush. Understory shrubs were dense over a fraction of 0.60 to 0.78 of their area (Table 11), and thus they were often pervasive and dense.

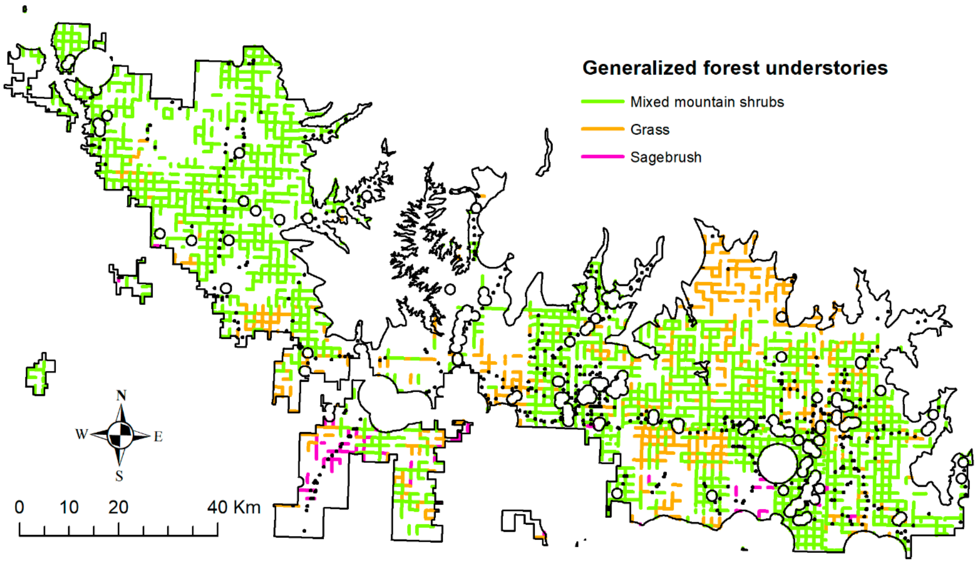

Figure 9. Generalized historical forest understories.

Table 10. Generalized forest understories recorded in section-line data.

	Pine and Piñon-Juniper		Pine		Dry Mixed Conifer		Moist Mixed Conifer	
Forest Understory	**All**	**Best** [1]	**All**	**Best**	**All**	**Best**	**Min.** [2]	**Max.** [2]
Grass (%)	21.2	42.1	11.8	15.5	9.0	14.6	0.9	3.1
Mixed mountain shrubs (%) [3]	22.2	44.1	63.4	83.1	52.4	85.4	27.5	96.9
Sagebrush (%)	7.0	13.8	1.0	1.3	0.0	0.0	0.0	0.0
No grass/shrub recorded (%)	49.6	-	23.8	-	38.6	-	71.6	-
Sample line length (km)	794	400	1911	1457	960	590	497	141

Notes: Within the section-line data, I selected and analyzed records in each zone only for surveyors who recorded understory shrubs and also recorded understory grass (Table S4). Thus, these records represent a sample of the zone. [1] The "Best" estimate is the percentage of all forest categories except "No grass/shrub recorded." This category is excluded because it likely is mostly composed of cases where the surveyor simply forgot to record the understory as was required. [2] In the case of moist mixed conifer, it is likely that the category "No grass/shrub recorded" could at times indicate a lack of understory grass or shrubs, rather than indicating a record where the surveyor forgot to record the understory as required. Thus, I bracketed the potential range by including this category to estimate a minimum and excluding it to indicate a maximum. [3] "Mixed mountain shrubs" refers to mixtures of shrubs typically dominated by Gambel oak, along with antelope bitterbrush, chokecherry, mountain mahogany, roundleaf snowberry, sagebrush, and Utah serviceberry. See Table 11 for more details about understory mixed mountain shrubs.

Table 11. General Land Office (GLO) section-line lengths in forests, with understory trees and shrubs having particular attributes, by forest zone.

Attribute	Pine and Piñon-Juniper	Pine	Dry Mixed Conifer	Moist Mixed Conifer
UNDERSTORY TREES[1]				
Fir (%)	0.00	0.00	0.25	0.00
Pine (%)	0.00	0.02	0.26	0.00
Pine-quaking aspen (%)	0.00	0.00	0.11	0.00
Quaking aspen (%)	0.88	1.11	13.23	12.93
Quaking aspen-pine (%)	0.00	0.00	0.18	0.00
Any tree (%)—sum of the above	0.88	1.13	14.07	12.93
Fraction of trees recorded dense	0.05	0.36	0.73	0.94
Total line length (km) with data	187.17	2374.41	1231.04	745.47
Percentage of line length in zone	17.48	73.85	68.48	78.01
UNDERSTORY MIXED MOUNTAIN SHRUBS[2]				
Gambel oak first (%)	90.01	99.14	98.85	98.43
Gambel oak present (%)	99.33	99.95	100.00	98.81
Roundleaf snowberry first (%)	0.00	0.00	0.00	0.00
Roundleaf snowberry present (%)	0.50	1.06	1.22	0.00
Sagebrush first (%)	8.50	0.83	0.00	0.00
Sagebrush present (%)	16.55	1.38	0.28	0.00
Utah serviceberry first (%)	1.49	0.03	1.15	1.57
Utah serviceberry present (%)	14.47	2.69	7.73	2.84
Fraction of shrubs recorded dense	0.74	0.60	0.70	0.78
Total line length (km) with data	273.70	1410.99	573.70	139.87

Notes: Within the section-line data, for the understory tree analysis, I selected and analyzed records in each zone only for surveyors who recorded understory trees (Table S4). Thus, these records represent a sample of the zone. For the analysis of mixed mountain shrubs, I selected and analyzed records in each zone only for surveyors who were rated at least "fair" in recording understory shrubs (Table S4). The sample is different from that in Table 10, because surveyors did not have to also record understory grass. [1] Percentages (%) are relative to total line length (km) with data. [2] Percentages (%) represent relative composition within only the mixed-mountain-shrub category given in Table 10, and thus they are not percentages of total forest line length.

3.3. Reconstructed Fire-Severity and Old Growth from Section-Line and Section-Corner Data

Some of the four sources of potential evidence of fire were contiguous and adjacent, and some boundaries were abrupt, but evidence of directional spread was limited (Figure 10a). Low severity, all from forest structure (Table 12), when overlain in GIS on topography, appeared associated with mesa tops and gentler slopes in the lower elevations of dry forests over some contiguous areas ≥10,000 ha (Figure 10a). Boundaries with scattered timber and non-forest were abrupt, suggesting adjoining severe fire. Mixed-severity areas, ~2/3 from forest structure and 1/3 from openings (Table 12) were smaller, not very contiguous or oriented, but often near low-severity areas (Figure 10a) in the two pine zones (Table 12). Most high-severity area from forest structure was in moist mixed conifer (Table 12) in some contiguous areas of 3000–6000 ha often sharply bounded by mixed- or low-severity areas (Figure 10a), suggesting fire.

About 2/3 of high severity from non-forest that became forested was in pine and dry mixed conifer (Table 12), with much in a contiguous area ≥40,000 ha in the northern part of the large western block (Figure 10a). Scattered timber occurred around it, and in several other cases around or adjacent to non-forest, particularly in the western half (Figure 10b). In other cases, these occurred in a finer mosaic, especially in the eastern half (Figure 10b). Beetle outbreaks/droughts are less likely than fire to have produced large areas of contiguous non-forest bounded sharply by scattered timber.

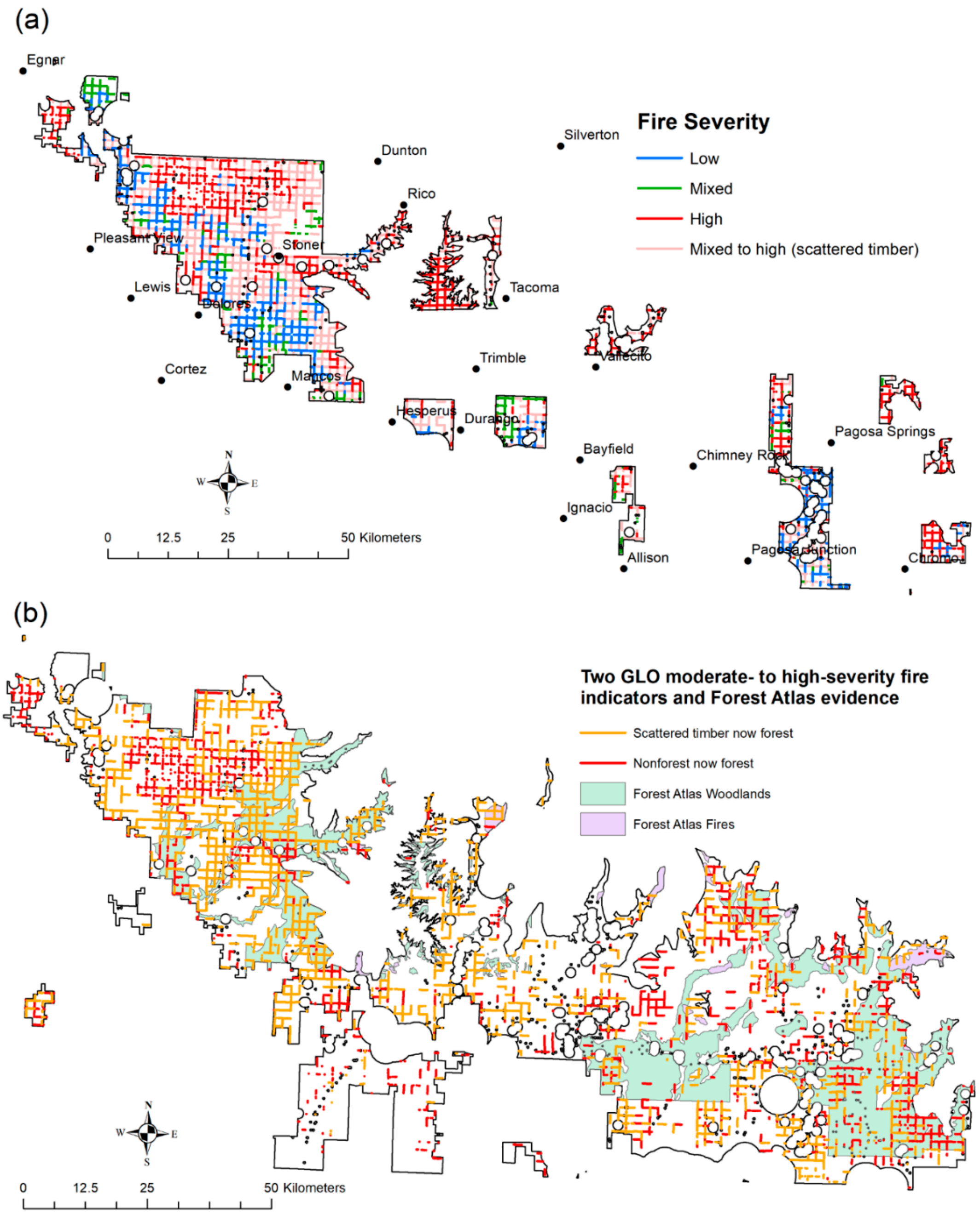

Figure 10. Reconstructed historical fire severity: (**a**) Based on section-corner and section-line data, and (**b**) based on only section-line data.

In both section-line and section-corner areas, recorded non-forest with: (1) dead/fallen/burned trees (87%–90% now forested), (2) small trees (69%–70%), or (3) shrubs and small trees (66%–76%), especially became forested by 2016 (Figure 11, Table 13). About 71%–73% of scattered timber also recovered to forest (Table 5). Thus, these four were good indicators of forest recovery by 2016; this recovery was underway in the historical period, and thus is not an artifact of fire exclusion. In contrast, only 35%–44% of shrubs and 15%–58% of grasslands became forested. Thus, they were much more persistent. These criteria together suggest fire was likely the major disturbance for the four, but some role for other disturbances (i.e., beetle outbreaks, droughts) cannot be fully excluded.

Using these sources, the montane in the section-corner area had 24% of area with exclusive low-severity fire, from 2% in moist mixed conifer to 21%–33% in the dry forest zones, including 33% in pine (Table 12, Figures S12–S15). Mixed-severity fire was found in 30% of the montane, with 34% in pine and 44% in pine and piñon-juniper (Table 12, Figures S12–S15). High-severity fire was found in 46% of the montane, 32%–35% in the two pine zones, 50% in dry mixed conifer, and 76% in moist mixed conifer (Table 12, Figures S12–S15). Estimated fire rotations for high-severity fire were 201 years in the montane, shortest (121 years) in moist mixed conifer, longest in the pine zones (260 and 284 years), and intermediate in dry mixed conifer (184 years). Pooled mixed- to high-severity fire had fire rotations of 121 years in the montane, 94 years in moist mixed conifer, 116 years in pine and piñon-juniper, and 138 years in the pine zone (Table 12).

Table 12. Reconstructed fire severities and fire rotations by zone within the section-corner area.

	Pine and Piñon-Juniper		Pine		Pine Zones	Dry Mixed Conifer		Dry Forests	Moist Mixed Conifer		Montane Overall	
Fire Severity Component[1]	**(km)**	**(%)**	**(km)**	**(%)**	**(%)**	**(km)**	**(%)**	**(%)**	**(km)**	**(%)**	**(km)**	**(%)**
Low severity-structure	24.3	21.0	288.3	33.4	31.9	106.9	23.4	29.2	6.6	1.9	426.1	23.9
Mixed severity-structure	22.5		83.7			16.2			14.8		137.2	
Mixed severity-openings	6.5		54.0			6.9			0.4		67.8	
Mixed severity-scattered[2]	21.7		157.2			97.8			61.6		338.3	
Total mixed severity	50.7	43.7	294.9	34.2	35.3	120.9	26.5	32.5	76.8	22.0	543.3	30.4
High severity-structure	0.0		22.1			19.3			144.7		186.1	
High severity-openings	8.5		18.8			8.5			5.3		41.1	
High severity-non-forest	10.8		81.4			102.8			54.3		249.3	
High severity-scattered[2]	21.7		157.2			97.8			61.6		338.3	
Total high severity	41.0	35.3	279.5	32.4	32.8	228.4	50.1	38.3	265.9	76.1	814.8	45.7
Sum of sources	116.0	100.0	862.7	100.0	100.0	456.2	100.0	100.0	349.3	100.0	1784.3	100.0
Total mixed + high severity	91.7	79.0	574.4	66.6		349.3	76.6		342.7	98.1	1358.1	76.1
Fire-rotation estimate[2]		**(yrs)**		**(yrs)**	**(yrs)**		**(yrs)**	**(yrs)**		**(yrs)**		**(yrs)**
High severity		260		284	280		184	240		121		201
Mixed- to high severity		116		138	135		120	130		94		121

[1] The components are: (1) structure-modeled fire severity from tree density and fraction of large and small trees, (2) openings-section corners with no recorded bearing trees on lines with either canopy density not recorded (high severity) or canopy dense/thick (mixed severity), (3) section-line length recorded as non-forest at the time of the surveys that by 2016 was forested, and (4) section-line length recorded as scattered timber at the time of the surveys that by 2016 was forested. [2] Fire rotation is calculated assuming that scattered timber that has recovered to forest represents mixed- to high-severity fire, and that 50% of this scattered timber represents mixed-severity fire and 50% represents high-severity fire. Fire rotation is calculated as 92 years/fraction burned. For example, in the pine zone, 0.342 + 0.324 burned at mixed- to high severity, for a total fraction burned of 0.666 in 92 years, and thus fire rotation for pooled mixed- to high severity was 92/0.666 = 138 years.

Old-growth forests were reconstructed to have covered 43% of a 101,648 ha analysis area and 53% of dry forests, from bearing trees at section corners (Figures 12 and 13a, Table 14). However, this is a sample only for the forested area where there were adequate bearing-tree data at section corners at the time of the surveys. Overall, this sample area was only 50.2% of 202,596 ha in the four forest zones in the unaffected section-corner analysis area (Table 1). The rest was openings and non-forest.

About 4% of old growth was in the pine and piñon-juniper zone (Figure S16), ~62% in pine (Figure S17), ~28% in dry mixed conifer (Figure S18), and ~7% in moist mixed conifer (Figure S19). About 59% of pine and 50% of dry mixed conifer in the analysis area was old growth, but only 12–22% of analysis areas in the other two zones (Table 14). Percentages of whole zones were smaller, only 7%–27%. Earlier analysis (Table 9) had shown large percentages of pines (32% in pine, 41% in dry mixed conifer) were ≥50 cm dbh in historical dry forests. Consistent with abundant old trees, much of the "not old growth" still contained 15–24 trees/ha ≥50 cm (e.g., Figure 12), half or more of the old-growth definition. Also, section corners with old growth were on section lines recorded as dense, thick, or heavily timbered over 52% of their length, and on lines recorded as scattered timber over 33% of their length (Table 14), with the remainder mostly not recorded, which included mature timber and old growth at corners and nearby. Some old growth was patchy; the ~1/3 recorded as scattered likely was disturbed at mixed to high severity, and some not-recorded area may indicate earlier disturbances that had partially recovered. Some old-growth patches were in 3000–5000 ha contiguous areas (Figures 12 and 13a). Early railroad logging targeted both the old-growth patches and adjoining patches with many large trees (Figure 12). Surveyors recorded direct observations of large trees in section-line descriptions (Table 4).

Table 13. Succession of historical non-forest (median survey year = 1881) to forest (circa 2016) by the zone with which non-forest was associated.

Non-Forest Now Forested[1]	Overall	Non-Forest Unknown[2]	Pine and Piñon-Juniper	Pine	Dry Mixed Conifer	Moist Mixed Conifer
Section-line area						
Mixed mt. shrubs (%)	43.7	45.0	59.7	37.7	54.7	51.1
Grasslands (%)	57.8	64.0	53.5	51.4	52.2	56.5
Dead/fallen/burned (%)	87.0	72.6	54.5	95.0	91.9	87.5
Small trees (%)	69.5	33.3	77.8	41.6	76.9	69.2
Sagebrush (%)	40.1	30.6	45.7	59.8	41.3	40.0
No timber (%)	48.8	54.3	23.5	44.5	65.1	82.5
Shrubs and small trees (%)	65.5	59.6	94.8	0.0	89.0	96.1
Mean (%)	56.5	51.3	55.4	45.4	78.1	69.3
Section-corner area						
Mixed mt. shrubs (%)	34.9	36.7	51.7	28.8	80.4	50.2
Grasslands (%)	14.6	32.7	27.1	42.7	80.4	15.2
Dead/fallen/burned (%)	90.4	100.0	-	93.3	80.4	86.7
Small trees (%)	69.2	53.9	77.8	59.2	80.6	57.7
Sagebrush (%)	45.4	40.0	19.6	50.4	-	-
No timber (%)	66.0	100.0	-	45.2	80.0	85.8
Shrubs and small trees (%)	75.5	72.0	94.8	0.0	86.0	100.0
Mean (%)	49.5	38.3	51.5	34.8	82.7	75.1

[1] Percentages are for the non-forest line length (km) present at the time of the surveys, that is now forested ca 201. [2] Non-forest unknown is where the corresponding forest zone could not be determined.

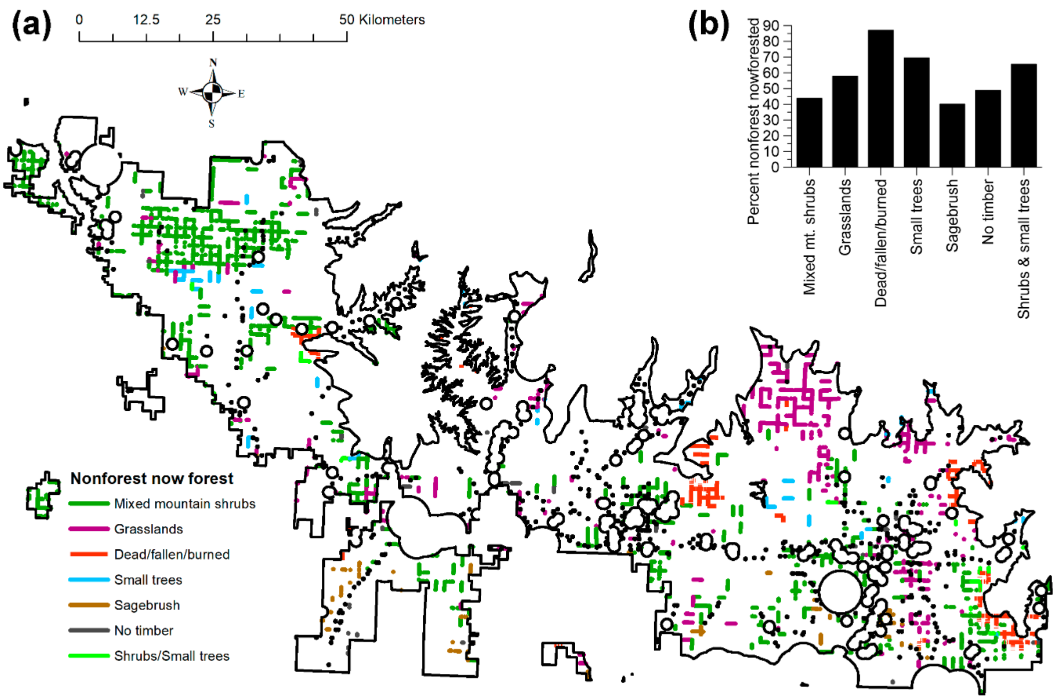

Figure 11. Succession of historical non-forest vegetation, with a median survey year of 1881, to forest, by ca 2016, across the whole section-line area: (**a**) The parts of the seven types of historical non-forest vegetation that had succeeded to forest about 135 years later, by circa 2016, the year of the Landfire map of existing vegetation, (**b**) Percentage of each of the seven types of historical non-forest vegetation that had succeeded to forest by ca 2016.

Table 14. Old-growth forests in the section-corner study area by zone and indicators on lines.

Zone	Analysis Area (ha)	Old Growth Area (ha)	% of Analysis Area	% of Whole Zone[1]	Lines-Heavily Timbered (%)[2]	Lines-Scattered Timber (%)[3]
Pine and piñon-juniper	7349	1623	22.1	12.3	57.3	28.1
Pine	45,986	27,129	59.0	26.1	61.8	28.5
Dry mixed conifer	24,467	12,316	50.3	26.5	37.0	45.9
Moist mixed conifer	23,846	2836	11.9	7.3	21.7	27.0
Dry forests	77,802	41,068	52.8	27.3	-	-
Overall	101,648	43,904	43.2	21.7	52.2	33.1

[1] Estimated unaffected areas by zone are given in Table 1 for the section-corner study area. [2] This is the percentage of all section-line segments that intersected old-growth polygons, where surveyors recorded the forest as dense, thick, heavily timbered, or using similar terms. [3] As in note 1, but where surveyors recorded the timber as scattered.

Reconstruction of old growth is confined to the section-corner area (Figure 13a), but it would be desirable to have some idea of the potential extent of old growth across the whole section-line area, as is roughly estimated in Figure 13b. The best indicators are forest line segments also recorded as dense, thick, heavily timbered, or using similar terms. Section lines recorded this way on average, in the section-corner area where this was analyzed, were 54% old growth and 82% had ≥15 trees ≥50 cm dbh/ha, more than half as many old trees as in old growth. Thus, these lines are reasonable indicators of old growth and areas with lots of old trees, but since ~1/3 of old growth was on line segments recorded as scattered timber, more areas likely had old growth.

3.4. Historical Cross-Validations of the Reconstructions

Historical tree density and basal area in the study area are known from only one tree-ring reconstruction in dry mixed conifer [40], but GLO tree data there were too poor to allow reconstruction. A single reconstruction is also insufficient for a general cross-validation, and thus just shows that tree-ring and GLO reconstructions are congruent, based on 29.6% RMAE for tree density and 13.3% RMAE for basal area (Tables S8 and S9).

The fire severity reconstructions can be cross-validated (Table S10). General cross-validation of the GLO estimate of 23% low, 27% mixed, and 50% high severity across dry mixed conifer landscapes, shows that tree-ring and charcoal reconstructions found a similar mix of these severities, although tree-ring/charcoal evidence is insufficient to accurately estimate percentages (Table S10). Also, where GLO reconstructions found 2% low, 22% mixed, and 50% high across moist mixed conifer landscapes, tree-ring and charcoal reconstructions found mostly mixed- and high-severity fire (Table S10). These general cross-validations suggest substantial congruence.

Fire severity reconstructions also allow three specific comparisons (Table S10). First, at Dolomite Lake near the southeastern boundary of the study area, Aoki [41] found evidence for mixed-severity fire in moist mixed conifer. The GLO reconstruction found both low and high severity, suggesting a mix of fire severities in that area, corroborating both studies. Second, Romme et al. [42] used stand-origin dating in aspen to estimate a historical aspen high-severity fire rotation of ~140 years northeast of Mancos, which the GLO data show was about 84% in historical dry mixed conifer. The GLO reconstruction, which had ~150 km of lines (and corners) in the montane part of their study area: (1) found 56% high-severity and 28% mixed-severity fire, confirming severe fires originated aspen, and (2) estimated a historical fire rotation of 110–165 years, which has an RMAE of 18%–21% relative to their 140 year rotation estimate (Table S10).

Third, the most significant specific cross-validation is for mixed- to high-severity fires from comparing GLO reconstructions (median 1881 date) and forest atlases (1908–1909), with a median 27–28 year difference. These two sources overlap on 164,087 ha (69.6%) of the 235,787 ha section-corner study area. I intersected, in ArcGIS, atlas woodlands and fires (Figure 10b) with the GLO fire severity reconstruction (Figure 10a) to map the cross-validation area (Figure S20), which had 2152 km of section-line length. This intersection provides only a rough comparison, as the atlases have RMSE spatial errors of about 600 m [7]. Nonetheless, atlas woodlands, described in 1904 as the aftermath of mixed- and high-severity fires [7], were confirmed here to be 84% GLO-reconstructed mixed- to high-severity fire area, 38% from scattered timber and 27% from non-forest that both became forested, 15% from forest structure, and 4% from forest openings. This cross-validation spans mixed- to high-severity fire area and woodland area in all four zones. The 16% of woodland area not from mixed- to high-severity fires was reconstructed to have been low-severity area with mature trees at the time of the surveys. This conversion to atlas woodlands could be spatial error, but more likely was from mixed- to high-severity fires after the surveys and before the atlases. Also, ~60% of reconstructed mixed- to high-severity fire area, including 2/3 of scattered timber recorded in surveys, did not end up mapped as woodlands or fires in atlases. A close look at atlases shows scattered timber was often mapped as "lien selection," "timber claim", or "homesteads/patents," but also some in the lowest timber-volume category. Since the GLO reconstruction extends back into the late-1700s, substantial area in the surveys indicating fires could already have been well forested or claimed for private use by the time of the atlases. The atlases and surveys have reconstruction periods that only overlap between 1850 and 1881 A.D. The upshot of this key cross-validation is that atlas woodlands are validated to largely be the aftermath of mixed- to high-severity fires, and the four sources used to reconstruct mixed- to high-severity fires from GLO surveys are also validated across all four zones. Conversion of mixed- to high-severity area to mapped private land uses means atlas woodlands underestimate prior mixed- to high-severity fires.

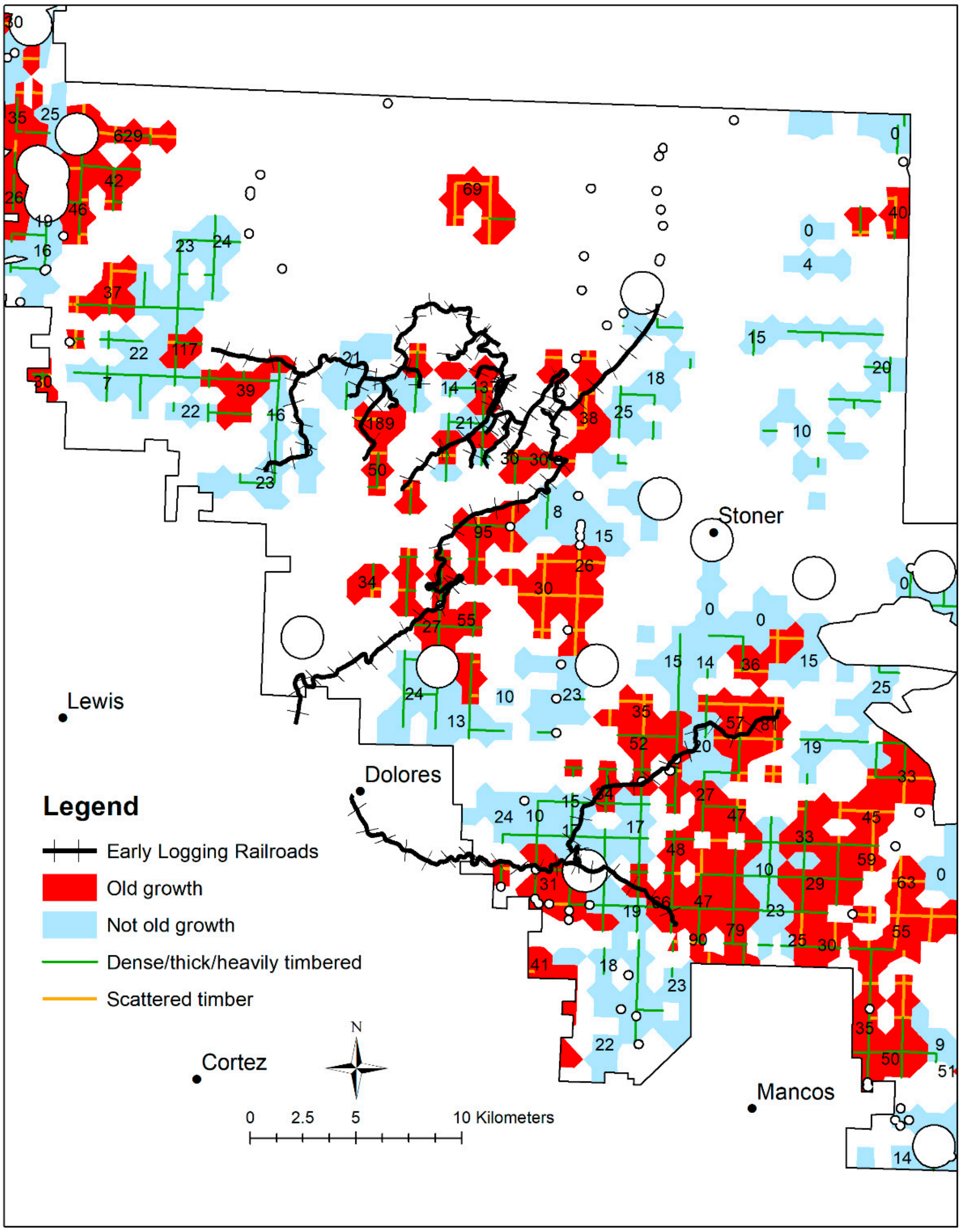

Figure 12. Old growth and not old growth in the western part of the old-growth analysis area. Numbers over polygons are the density (trees/ha) of trees that meet the diameter criteria for old-growth trees. Section lines recorded as dense, thick, or heavily timbered included old growth, but extended out into polygons with fewer than the minimum density of large trees necessary to qualify as old growth. About 1/3 of old growth was not continuous forest, but instead scattered timber. Early railroads, from [7], were directed at the large timber available in and near the old-growth areas.

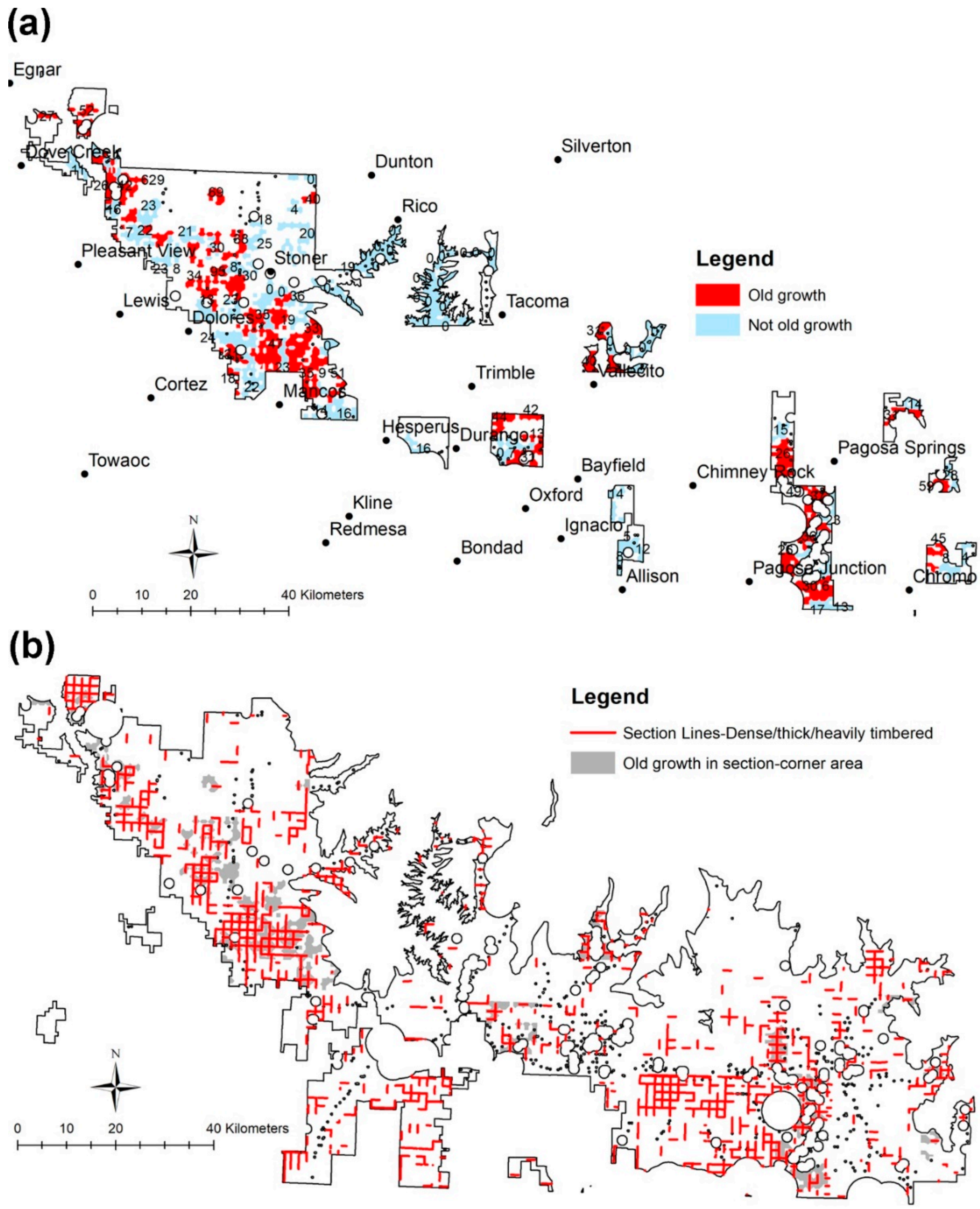

Figure 13. (**a**) Reconstructed old-growth forests in the section-corner area. (**b**) The best indicator of potential old growth across the whole study area is from section-line descriptions that recorded the forest as dense, thick, heavily timbered, or using other similar terms. These lines, in the section-corner area, were ~54% old growth and 82% of section-line length had ≥15 trees ≥50 cm dbh/ha, and so these lines mostly had abundant old trees.

Early scientific reports and observations from the surveyors in the study area (Table 4) and from early reports in the study area and the broader region (Table S7) further corroborate the fire severity and forest-structure reconstructions. High-severity fire was directly recorded by the surveyors in the study area in all zones, including in pine forests (Table 4). Moderate to high-severity fires in mixed conifer areas are confirmed in both the study area and region to have led to dense young aspen, dense shrubs and understory conifers, accompanied by scattered remnant trees from the pre-fire forest (Table S7: Q1–Q3, Q8–Q9, Table 4). This general structure of scattered timber, without reporting that fire caused it, was also reported (Q6). Mixed conifer forests in the study area and region were reported to have had varying age classes and densities, including young pole stands with surviving older trees, and open, park-like old-growth forests, confirming GLO findings here of a variety of low, moderate, and high-severity fires (Table S7).

The old-growth reconstruction (e.g., Figure 12) is corroborated in four ways. First, the early logging railroads clearly were aimed at areas with old growth, possibly even old growth with the most large trees (Figure 12), substantiating that these were areas with large timber. Second, the woodlands mapped in early forest atlases [7], which were described as severely burned, are generally in areas outside mature forests identified by GLO data in the late-1800s (Figure S21). This corroborates that reconstructed old-growth forests and adjoining non old growth, do identify mature forests, since many were still present in 1908–1909. This also substantiates that forest atlas woodlands were not areas of mature forests, consistent with their early description as having been burned severely [7]. Third, surveyors often directly recorded large trees, good timber, or dense/thick/heavily timbered areas suggestive of old trees and old forests (examples in Table 4). Finally, the method of old-growth reconstruction follows [35], which found old growth historically over 76% of a large area in Oregon; this was corroborated by a later survey that found 78%–82% [35]. Corroboration also came from a tree-ring reconstruction that found 48–52 large trees/ha where GLO data found a median 54.6 large trees/ha [35]. These further validate the accuracy of the method.

4. Discussion

4.1. Historically Variable Fire Severity

Historical ponderosa pine and mixed conifer forests across the West are increasingly understood to have had variable or mixed historical fire severities [2,43,44]. Multiple sources show this: (1) GLO-reconstructions [1,3,19,22,24,25,45,46], (2) paleo-charcoal reconstructions (reviewed in [47]), (3) landscape-scale aerial-photos [6], (4) landscape-scale tree-ring reconstructions (e.g. [48,49]), (5) landscape-scale forest atlas data [7], and (6) early scientific reports across large landscapes [5,32].

Fire severity reconstructions here also show this mixture of fire severities across all zones (Table 12), and found the mixture was similar to the mixture in some nearby landscapes. The San Juan's dry forests, with 29% low, 33% mixed, 38% high, and a 240 year high-severity fire rotation (Table 12), was very similar to the Colorado Front Range, which was modeled, based on tree-ring data, to have had ~28% low severity, 36% mixed severity and 36% high severity [48]. Our Front Range GLO study area was small and had more high-severity fire [1]. Black Mesa, northern Arizona, which stands out in northern Arizona for its 12% low, 33% mixed, 55% high, and 217 year high-severity fire rotation [3], was also similar. Other northern Arizona areas had more low-severity area and longer high-severity fire rotations. The Uncompahgre Plateau, just to the north, had little low-severity and more high-severity fire [3].

Exclusive low-severity fire (Figure 10a) over 24% of the montane was mostly in dry forests, 32% of pine zones and 23% of dry mixed conifer (Table 12), largely on mesas and gentler southerly-facing slopes at lower elevations, as in the Colorado Front Range [48]. Fire-history data at 33 sites [7] showed historical low-severity fire rotations were 16–59 years (median 31 years) in pine and 20–496 years (median 78 years) in dry mixed conifer. Frequent fire (low-severity fire rotations <25 years), which kept fuel loads down, was at four of nine sites (44%) in pine, roughly similar to the 32% of pine zones with exclusive low-severity fire found here. Exclusive low-severity fire over 23% of dry mixed conifer is congruent with the three of 15 (20%) dry mixed conifer sites with low-severity fire rotations <30 years on southerly-facing slopes at lower elevations [7]. Agreement corroborates both sources. Overall, frequent low-severity fire, based on tree-ring data, occurred on only 15% of the montane and less than half the pine zones [7], also similar to the Colorado Front Range. Exclusive low-severity fire, which included some longer fire rotations, was found on 24% of the montane (Table 12), again similar to the 28% in the Colorado Front Range [48].

Mixed-severity fires, 30% of the montane, highest in the two pine zones (Table 12), appeared most common within and adjoining low-severity fire areas and scattered timber, and between larger patches of low and higher severity (Figure 10a), supporting the transitional nature of mixed severity. High-severity fires were in contiguous blocks (Figure 10a), particularly in mixed conifer. Half of dry mixed conifer and 3/4 of moist mixed conifer burned at high severity in the 19th century, not unlike the 54%–57% burned in these forests on the Uncompahgre Plateau [22]. Forest atlases from 1908–1909 also show contiguous areas of severe fire in the San Juan montane [7] congruent with this study. This study found more mixed- to high-severity fire, which is likely underestimated by the atlases, but mixed- and high-severity fire estimates here are strongly shaped by extensive scattered timber (Table 12), and its rough assignment as 50% mixed and 50% high. In other areas [22], more evidence was available about its severity, and use of scattered timber as an indicator of fire was not restricted to just recovered forest area.

The 19th-century severe fires in mixed conifer forests are the primary source of extensive (and beautiful) aspen forests that remain prominent in the region [29,30,42,49,50]. Major droughts and alignment of ocean-atmosphere teleconnections favored fire in the southern Rockies in the last half of the 19th century ([32], Figures 10–13), [51]. Millions of acres of forests reportedly burned on the western slope in Colorado (Table S7: Q14–Q15). Severe fires also occurred in montane and subalpine forests in the nearby Sangre de Cristo Mountains and higher-elevation forests in the Jemez Mountains in New Mexico [52]. Short mixed- to high-severity fire rotations of 94–138 years in forests in the study area (Table 12), may reflect this exceptional period and be atypical of longer patterns.

The occurrence of episodes of severe fire supports the hypothesis that Arizona to Colorado is a tension zone, where rapid transformations from episodes of disturbance can leave different nearby landscapes [3]. Areas of open, low-density dry forests could have been permanent in some cases, maintained by low-and mixed-severity fires. But, more likely, based on very different nearby landscapes (Mogollon and Black Mesa, San Juan and Uncompahgre), is that periods of low-severity fires with somewhat higher intensity can result in very open forests that resist higher-severity fire for a while, but subsequently recover to higher density, before another severe fire [6,24,32,53]. Evidence here includes: (1) large areas of scattered timber, likely from mixed- to high-severity fire, (2) unusually extensive low-density pine forests likely from intense low- or mixed-severity fires, and (3) some dense forests, likely recovering from earlier severe fires. Episodic droughts, dense shrubs, exposed topography oriented southwest and aligned with prevailing winds [7], and high topographic diversity likely also played significant roles in shaping highly variable fire severity, as they did in somewhat different ways in nearby mountain ranges [22,48]. The likely reality of this tension zone is that seemingly stable forest structures (e.g., open, low-density, old-growth forests) in this zone were historically vulnerable to rapid transformation in episodes of severe fires.

4.2. Historically Heterogeneous Forest Structure

Varying historical fire severities led to heterogeneous forest structures that were likely a key source of biological diversity, as well as natural resistance and resilience, in San Juan montane landscapes, as elsewhere [54,55]. Historical dry forests in the San Juans were roughly similar in tree density to some other dry forests in the western USA with landscape-scale reconstructions [3], particularly dry forests in northern Arizona. Historical median tree density of 118 trees/ha for trees ≥ 10 cm dsh) in dry forests in the San Juans is very similar to the 121 trees/ha on the Coconino Plateau [46] and 124 trees/ha on the Mogollon Plateau [1] in northern Arizona. Higher median tree density included 137 trees/ha on Black Mesa [1], 162 trees/ha in the Colorado Front Range [1], and 183 trees/ha on the Uncompahgre Plateau [22]. Sierran-Cascade forests were much denser [3].

San Juan dry forests were more heterogeneous in tree density and had more dense forests than in northern Arizona. The coefficient of variation (CV) in tree density was 45%–54% in northern Arizona [46], but 99% in the San Juans (Table 6). Higher variability in tree density may be from greater topographic diversity and/or more diverse fires that led to both more open and dense forests. Open forests with <100 trees/ha covered 42% of dry forests and 46% of pine zones in the San Juans, much more than the 19% on the Coconino Plateau, 24% on Black Mesa, and 33% on the Mogollon Plateau [46]. In the San Juans, 29% of dry forests were dense (>200 trees/ha), more than the 16%–18% dense forests in northern Arizona [46]. However, the San Juans had more dry mixed conifer, which was 50% dense. In pine only, dense forests were similar in the San Juans (19.4%) and northern Arizona (16–18%). Very dense forests (>300 trees/ha), however, stand out in the San Juans, occurring over 19% of dry forests, including 9% of pine forests and 36% of dry mixed conifer forests (Table 6).

Also, San Juan montane forests included denser zones. First, pine and piñon-juniper and dry mixed conifer zones had means of 303 and 245 trees/ha, medians of 209 and 200 trees/ha, and 54% and 50% of these zones, respectively, with dense forests of >200 trees/ha (Table 6). Second, preliminary data for moist mixed conifer show this zone to have historically had very dense forests, with a mean of 435 trees/ha and median of 286 trees/ha, and dense forests over 66% of this zone (Table 6). On the Uncompahgre Plateau, these forests had a similar mean of 422 trees/ha, median of 284 trees/ha, and dense forests over 52% of the zone [22], congruent evidence of dense forests.

Historical basal area was also similar to that in northern Arizona. Basal area on the Coconino Plateau had a mean of 11.3 m^2/ha, a median of 10.9 m^2/ha, and ~12% of forest area had >15 m^2/ha [46]. This is very similar to the mean of 11.5 m^2/ha and median of 10.2 m^2/ha in pine in the study area, with about 17% of pools having >15 m^2/ha (Table 7). In contrast, the Uncompahgre Plateau had a low median basal area (only 6.5 m^2/ha) in dry mixed conifer forests and 74% of area with <8 m^2/ha from severe late-1800s fires [22]. Median basal area in moist mixed conifer forests here was only 8.4 m^2/ha, also likely from severe fires. Pine and piñon-juniper had a higher mean basal area (12.8 m^2/ha) than in purer pine (11.2 m^2/ha) and more forest area with >15 m^2/ha (30% vs. 15%). Overall, 20% of the montane and 21% of dry forests had >15 m^2/ha. This is little compared to Sierran mixed conifer forests, which had median basal areas of 25%–38 m^2/ha [19]. Spatial variation in basal area (CV) was 39%–76% (Table 7), lower than for tree density, but larger pools reduce CV. Historical median QMDs were 34–44 cm in dry forests (Table 7). Thus, the tree of mean basal area was less than about a century old. Median QMDs were 44.2 cm in pine, only a little larger than the 39.8 cm for ponderosa on the Coconino Plateau [46].

Definitions used to distinguish zones play a significant role in compositional patterns (Table 8). For example, Tepley and Veblen [49] found high levels of shade-tolerant trees, with white fir and Douglas-fir more abundant than ponderosa pine in dry mixed conifer in the eastern part of my study area. I placed lines with pine recorded third into moist mixed conifer, and so some of Tepley and Veblen's dry-mixed conifer stands could have ended up in moist mixed conifer here. However, 25% of dry mixed conifer did still have substantial (mean = 22%) shade-tolerant trees, up to 70%. Also, my sample is limited near Tepley and Veblen's sites, but shade-tolerant conifers were abundant near there (Figure 7). In contrast, Wu's [56] dry mixed conifer was defined by a structure shaped by low-severity fire where shade-tolerant trees seldom reached the tree canopy. It appears that I generally used mixed conifer definitions between these studies.

Historical montane forests were not numerically dominated by large trees, but instead small trees <40 cm dbh (Figure 8) that were 70% of all trees and 51% of all pines. This was also found in GLO studies over 1.7 million ha in seven dry-forest landscapes with data from 45,171 trees [57]. Small trees historically provided key advance regeneration that enhanced forest resilience to canopy mortality in droughts and insect outbreaks, more significant recent mortality agents than are fires [55,57]. A peak in the 30–40 cm diameter class, in pines, was also found on the Uncompahgre Plateau [22] (Figure S17), but not other study areas [57]. These peaks suggest regional natural disturbance episodes and subsequent pluvials or fire quiescence [58] in the early 1800s. Aspen had inverse-J diameter distributions in mixed conifer (Figure 8), as on the Uncompahgre Plateau [22] (Figure S17), also suggesting regional episodes of high-severity fires that initiated aspen in ~1820–1880 [28–30]. A peak in the 20–30 cm class for shade-tolerant trees in mixed conifer (Figure 8) was also on the Plateau [22] (Figure S17). Regionally congruent periods of disturbances are thus apparent, further suggesting the possibility that adjoining mountain ranges could be vulnerable to sudden transformation.

Old-growth forests covered 43% of montane forests and 53% of dry forests, but only about half of these percentages if the whole zone is considered, which is much less than the 76% in eastern Oregon dry forests [35]. Nonetheless, large trees still very substantially shaped the ecology of historical San dry forests. Large pines (e.g., >50 cm) historically were prominent components of San Juan dry forests, making up about 1/3 of pines in the two pine zones and 41% of pines in dry mixed conifer (Table 9). Biological diversity and ecological attributes of the few extant old-growth forests in the San Juans were reviewed in Romme et al. [59], who later [12] found most old growth in dry forests had been subjected to high-grade logging, including railroad logging (e.g., Figure 12), where large trees were effectively liquidated before ~1950. Old-growth forests were high-graded into the 1980s [14] and suffered from other mortality [12]. In the railroad-logged part of Figure 12, Romme et al. found, in 1994 ~45 years after railroad logging ended, only ~6% of ponderosa pines were >40 cm dbh [12]. In contrast, GLO data show that historically ~46% of ponderosa pines in pine forests and ~59% of ponderosa pines in dry mixed conifer forests were >40 cm (Table 9). Large trees likely remain significantly deficient across dry forests in the San Juan Mountains.

Understory seedlings/saplings were present in forests over only ~1% of the two pine zones, but ~13% of mixed conifer (Table 11). Almost all were quaking aspen, except pine and fir on <1% of dry mixed conifer. Dubois [16] (p. 9) said of ponderosa in the western San Juans: "In the virgin forest and in the poor open stand on thin soil there is practically no reproduction." Dubois [15] (p. 7) described dry forests in the central and eastern study area: "Reproduction of bull pine is poor. In many places groups of seedlings are coming in, but in the large blanks made by cutting, restocking is slow." Bull pine is young, but established ponderosa pine. Regeneration of ponderosa was variable, but often poor in the Southwest in general [55]. Near absence of seedling/sapling conifers in dry forests in the San Juans also suggests extended unfavorable climate or fires that had recently prevented or removed coniferous seedlings/saplings. Conifer regeneration is favored in southwestern dry forests by canopy disturbances and periods without fire and/or with abundant moisture [58]. In contrast, dense understory aspen in mixed conifer forests with larger surviving trees suggests severe fires before the surveys. This understory aspen in ~13% of mixed conifer forests was recorded as "dense" over 73–94% of line length (Table 11). Surveyor records specifically show dense small aspen occurred after severe fires (Table 4). Early observations in regional forests also show these forests often had abundant dense aspen in the understory after severe fires (Table S7: Q2–Q3, Q8–Q9). Tree-ring dating on the Uncompahgre Plateau, where aspen was also dense in mixed conifer understories, showed many aspen originated after severe fire in 1879 [22,30].

Understory shrubs were found historically on 83%–85% of pine and dry mixed conifer area (Table 10) and were dense over a fraction of 0.60 to 0.70 of that area (Table 11). Shrubs occurred on only 44% of pine and piñon-juniper but were still dense on a fraction of 0.74 of that area and occurred on an uncertain amount of moist mixed conifer (Table 10). Most other historical dry forests had low shrub abundance and low- to moderate dense fractions, respectively, including the Colorado Front Range (<1%, 0.00), Black Mesa, Arizona (7%, 0.00), Mogollon Plateau, Arizona (11%, 0.09), and Blue Mountains, Oregon (18%, 0.58) [1]. Only the Eastern Cascades, Oregon (58%–83%; [24]) equaled abundance here, and it was only exceeded on the Uncompahgre Plateau (79%–90%; [22]) and in the western Sierra (86%–99%; [19]). Shrubs were even denser on the Uncompahgre Plateau (0.81–0.96), but were much less dense in the Cascades (0.23–0.54) and Sierra (0.16–0.46) than here (0.60–0.78). Gambel oak here was most common in mixed mountain shrubs, with some Utah serviceberry and small amounts of roundleaf snowberry. Sagebrush was also common in pine and piñon-juniper (Table 11). Efforts to reduce these shrubs, assuming frequent fire kept them at low levels, are not generally supported. Fire was frequent only in the lowest parts of ponderosa pine and dry mixed conifer zones [7]. Most of these shrubs resprout readily after fires [32], and surveyors reported dense shrubs after severe fires (e.g., Table 4). Pervasive and often dense understory mixed mountain shrubs were a historical feature of dry forests and other parts of montane forests in southwestern Colorado.

4.3. Landscape-Scale Fire and Forest Management

GLO reconstruction of fire severity and evidence from forest atlas data and early records (Table 12, [7]) provide previously unavailable landscape-scale evidence that mixed- and high-severity fires were historically characteristic of all zones in the montane (Table 12, Figures S12–S15). These fires have declined; for example, high-severity fires between 1984–2012 burned in the area with long fire rotations of 1816 years in ponderosa and 926 years in dry mixed conifer [47], a much lower rate than historical high-severity fire rotations of 280 years in pine and 184 years in dry mixed conifer (Table 12). Historically, severe fires likely produced much of the forest openings, non-forest, and scattered timber recorded in the surveys (Tables 5, 12 and 13) and most of the early-successional woodlands recorded in forest atlas data [7]. Creation and maintenance of complex early seral forests (CESFs), the early-successional stages after severe fires, have thus declined (Figure 11). CESFs are significant, supporting a broad array of generalist and specialist plants and animals, complex food webs, and high biological diversity [60]. Uncharacteristically low rates of mixed- to high-severity fires have likely adversely affected montane landscapes by reducing CESFs and non-forest as well as landscape diversity and landscape resilience needed at a time of impending effects from climate change [55].

Proposals for intensive fuel reduction and mechanical restoration of forest structure in upper elevation ponderosa pine and in mixed conifer forests in Colorado [61] have little basis, are likely ineffective, and are also difficult or infeasible. For example, evidence in [61] is unfortunately biased and unreliable; it was primarily from logged forests, which can erase historical fire evidence. Extensive evidence of historically severe fires had already been found in a large sample of unlogged sites in the Colorado Front Range [48] and from entry-exit records from early land surveys across 624,156 ha of the Front Range [45], a large body of direct historical evidence overlooked by Battaglia et al. [61]. These fires were not, through 2012, occurring at rates that exceeded historical rates, although more fire is expected [47]. Moreover, thinning has been extensively implemented in western dry forests, but fires are still increasing; thinning is likely often ineffective because even large fires seldom encounter fuel reductions [62]. Finally, fires in Colorado's historical upper montane landscapes were so temporally and spatially complex, even at times at a fine scale [49], it is likely extremely difficult if not infeasible to restore these landscapes with logging and/or thinning.

Restoring historical fire is likely the most feasible long-term fire-management approach in the upper half of the pine zones and in mixed conifer, although it entails high fire-management skill combined with sophisticated adaptive resilience for residents and infrastructure. New methods for living with fire [62,63] are essential where historical fire was dangerous, as in these zones. Restoring historical fire could have significant other benefits, including restoring CESFs and non-forest that have likely declined. Evidence from a large study suggested that the most feasible long-term approach to indirectly limit bark beetles is to maintain: " ... heterogeneous landscapes composed of stands with heterogeneous structures and containing densities in the neighborhood of 80 feet^2 [18.4 m^2/ha] of basal area" [64] (p. 157). Since historical mean basal area was <12.9 m^2/ha across all montane zones in the study area, and 3/4 or more of montane landscapes had <18.4 m^2/ha of basal area (Table 7), restoring fire should also increase resistance and resilience to beetle outbreaks.

An exception where active restoration of forest structure is worthwhile and feasible is in the lower part of the pine zones and a small part of dry mixed conifer, generally on mesas and gently sloping sites, where exclusive low-severity fire, found in this study (Figure 10, Figures S12–S15), coincided with independent evidence of historical low-severity fire rotations of <30 years [7]. These sites often also had old-growth forests or abundant old trees (Figure 12) and relatively low tree density (Figure 6). Large old trees that resist fires and provide resilience (seed) after fires are not easily replaceable, but abundant middle-aged trees here likely mean significant progress could be achieved in the few decades before the U.S. needs to have reached net-zero for carbon emissions [55]. Restoring old growth and historical fire, guided by the historical variability shown here and in other sources [12], would be ecologically valuable and timely, increasing the variability in forest structure that provides landscape resistance and resilience [55] as fire increases with climate change. Evidence here adds support to the idea that historical landscapes in a tension zone from Arizona to Colorado had imperfect resistance to episodes of severe fires, suggesting that restored montane forests will have increased resistance and resilience, but will remain dangerous places to live.

Evidence that historically severe fires occurred in all zones of the study area means that multiple coordinated efforts are warranted [62,63] to increase the resistance and resilience of both people and nature to the severe fires that occurred and are likely to increase with climate change. This could include: (1) expediting the completion of explicit defenses around and near all highly valued resources and assets, including the entire wildland-urban interface, (2) planning and other methods to limit further expansion of the wildland-urban interface into these dangerous forests, (3) a rapid warning and systematic evacuation system in case of advancing severe fires, (4) active restoration of old-growth forests in the lower part of the pine zones with both prescribed and natural fires, and (5) active restoration of natural fire in the upper part of the pine zone and in mixed conifer zones. It is sensible to move from reducing fire severity and stopping fires everywhere, which are ecologically damaging and increasingly infeasible, to fostering living with fire in restored and resilient forest landscapes with resilient fire-adapted human communities and associated infrastructure. Spatial datasets used in the study (Data S1) could help in creating parts of a systematic, coordinated plan.

5. Conclusions

This study found evidence from early land surveys, mostly done by 1887 before extensive expansion of land uses, that episodes of mixed- to high-severity fires, likely associated with regional climate episodes, occurred in the 19th century over about 76% of ponderosa pine and mixed conifer landscapes. This supports the hypothesis that the study area was part of a regional tension zone from Arizona to Colorado that was vulnerable to transformation in episodes of mixed- to high-severity fires. The possibility of these fires is increased by the study area's historically dense understory shrubs, exposed topography oriented southwest in alignment with prevailing winds, and high topographic diversity. Forests with few large trees, and large areas of scattered timber and open shrublands and grasslands that have now recovered to forest, are indicators of these fires, which are corroborated by independent evidence. In contrast, about 32% of pine and 24% of dry mixed conifer zones had evidence of mature forests and only low-severity fires. These mature forests were typical of regional mature historical forests, particularly in northern Arizona, with low—to moderate tree densities and basal areas, including open, old-growth forests over about half their area.

Today's montane forest landscapes likely are still generally recovering from 19th-century mixed- to high-severity fires, with some now reaching middle to older ages. However, large trees in the mature and old-growth forests, present at the time of the surveys, were lost to later fires in some cases, but most were likely logged by the 1950s–1980s, also leaving recovering middle-aged forests. Homogenized, often middle-aged, recovering forests over large areas now face a future of increasing fire, drought, and insect-outbreak episodes with climate change. The most feasible ecological restoration and management in the face of these increasing episodes may be to focus on restoring and managing wildland fires for resource benefit, supplemented by prescribed fires, in the upper part of the pine zones and most of mixed conifer, and using active management to restore fire-resistant old-growth forests in the lower part of the pine zones. These two approaches have the greatest chance to increase stand- and landscape-scale resistance and resilience to disturbances in the next few decades. However, nearby communities and infrastructure would also benefit from becoming fully fire adapted. Incomplete historical forest resistance suggests that it may be difficult to stop episodes of future mixed- and high-severity fires from burning into communities and infrastructure.

Supplementary Materials: The following are available online at http://www.mdpi.com/2073-445X/9/1/3/s1. Table S1: Tree names used in the study and by surveyors in line and corner data, Table S2: Vegetation and land-use information in township descriptions, Table S3: Shrub names used in the study and by surveyors in line data, Table S4: Information recorded by surveyors in the study area, Table S5: Equations used in the reconstructions, Table S6: Landfire existing vegetation types (LF 2.0.0-circa 2016 data) used to identify modern upland forests, Table S7: Early observations (up to about 1920) about historical fire and forest structure in forests in and near the study area, Table S8: General cross-validation of the historical GLO median tree density estimate with the only available tree-ring estimate of historical tree density for the study area, Table S9: General cross-validation of the historical GLO median basal-area estimate with the only available tree-ring estimate of historical basal area for the study area, Table S10: GLO-based reconstructions of fire severity and high-severity fire rotation cross-validated with tree-ring and charcoal estimates, Figure S1: Reconstructed tree density (trees/ha) for sample ponderosa pine and piñon-juniper forests in the study area, Figure S2: Reconstructed tree density (trees/ha) for sample ponderosa pine forests in the study area, Figure S3: Reconstructed tree density (trees/ha) for sample dry mixed conifer forests in the study area, Figure S4: Reconstructed tree density (trees/ha) for sample moist mixed conifer forests in the study area, Figure S5: Reconstructed tree density (trees/ha) for sample dry forests in the study area, Figure S6: Reconstructed basal area (m2/ha) for sample ponderosa pine and piñon-juniper forests in the study area, Figure S7: Reconstructed basal area (m2/ha) for sample ponderosa pine forests in the study area, Figure S8: Reconstructed basal area (m2/ha) for sample dry mixed conifer forests in the study area, Figure S9: Reconstructed basal area (m2/ha) for sample moist mixed conifer forests in the study area, Figure S10: Reconstructed basal area (m2/ha) for sample dry forests in the study area, Figure S11: Reconstructed quadratic mean diameter (QMD) in montane forests in the study area, Figure S12: Reconstructed fire severity in the ponderosa pine and piñon-juniper zone, Figure S13: Reconstructed fire severity in the pine zone, Figure S14: Reconstructed fire severity in the dry mixed conifer zone, Figure S15: Reconstructed fire severity in the moist mixed conifer zone, Figure S16: Reconstructed old-growth forests of the pine and piñon-juniper zone in the study area, Figure S17: Reconstructed old-growth forests of the pine zone in the study area, Figure S18: Reconstructed old-growth forests of the dry mixed conifer zone in the study area, Figure S19: Reconstructed old-growth forests of the moist mixed conifer zone in the study area, Figure S20: Cross-validation of the GLO fire severity reconstruction with woodlands and fires mapped in early forest atlases, Figure S21: Cross-validation of the GLO old-growth reconstruction with woodlands, representing mixed- to high-severity fires, mapped in 1908–1909 forest atlases, Text S1: Limitations and critiques of GLO reconstructions, and Data S1: The datasets used in the study.

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References

1. Williams, M.A.; Baker, W.L. Spatially extensive reconstructions show variable-severity fire and heterogeneous structure in historical western United States dry forests. *Glob. Ecol. Biogeogr.* **2012**, *21*, 1042–1052. [CrossRef]
2. Odion, D.C.; Hanson, C.T.; Arsenault, A.; Baker, W.L.; DellaSala, D.A.; Hutto, R.L.; Klenner, W.; Moritz, M.A.; Sherriff, R.L.; Veblen, T.T.; et al. Examining historical and current mixed-severity fire regimes in ponderosa pine and mixed-conifer forests of western North America. *PLoS ONE* **2014**, *9*, e87852. [CrossRef] [PubMed]
3. Baker, W.L.; Williams, M.A. Land surveys show regional variability of historical fire regimes and dry forest structure of the western United States. *Ecol. Appl.* **2018**, *28*, 284–290. [CrossRef] [PubMed]
4. Covington, W.W.; Moore, M.M. Southwestern ponderosa forest structure: Changes since Euro-American settlement. *J. For.* **1994**, *92*, 39–47.
5. Baker, W.L.; Veblen, T.T.; Sherriff, R.L. Fire, fuels and restoration of ponderosa pine–Douglas-fir forests in the Rocky Mountains. *J. Biogeogr.* **2007**, *34*, 251–269. [CrossRef]
6. Hessburg, P.F.; Salter, R.B.; James, K.M. Re-examining fire severity relations in pre-management era mixed conifer forests: Inferences from landscape patterns of forest structure. *Landsc. Ecol.* **2007**, *22*, 5–24. [CrossRef]
7. Baker, W.L. Historical fire regimes in ponderosa pine and mixed-conifer landscapes of the San Juan Mountains, Colorado, USA, from multiple sources. *Fire* **2018**, *1*, 23. [CrossRef]
8. Schulte, L.A.; Mladenoff, D.J. The original US public land survey records: Their use and limitations in reconstructing presettlement vegetation. *J. For.* **2001**, *99*, 5–10.
9. Butler, S.A.; McDonald, L.L. Unbiased systematic sampling plans for the line intercept method. *J. Range Manag.* **1983**, *36*, 463–468. [CrossRef]

10. U.S. Bureau of Land Management. Data Navigator. Available online: https://navigator.blm.gov/home (accessed on 24 October 2019).
11. Livermore, M. *Fictitious Surveys*; P.O.B. Publishing Co.: Canton, MI, USA, 1991.
12. Romme, W.H.; Floyd, M.L.; Hanna, D. *Historical Range of Variability and Current Landscape Condition Analysis: South-Central Highlands Section, Southwestern Colorado & Northwestern New Mexico*; Colorado Forest Restoration Institute, Colorado State University: Fort Collins, CO, USA, 2009.
13. Baker, W.L. Indians and fire in the Rocky Mountains: The wilderness hypothesis renewed. In *Fire, Native Peoples, and the Natural Landscape*; Vale, T.R., Ed.; Island Press: Washington, DC, USA, 2002; pp. 41–76.
14. Paulson, D.D.; Baker, W.L. *The Nature of Southwestern Colorado: Recognizing Human Legacies and Restoring Natural Places*; University Press of Colorado: Boulder, CO, USA, 2006.
15. Dubois, C. *Report on the Proposed San Juan Forest Reserve, Colorado*; Unpublished Report; San Juan National Forest: Durango, CO, USA, 1903.
16. Dubois, C. *The Proposed Montezuma Forest Reserve: Examination, Report, and Recommendations*; Bureau of Forestry, U.S. Department of Agriculture, National Archives and Records Administration: Broomfield, CO, USA, 1904.
17. Chappell, G.S. *Logging along the Denver & Rio Grande: Narrow Gauge Logging Railroads of Southwestern Colorado and Northern New Mexico*; Colorado Railroad Museum: Golden, CO, USA, 1971.
18. Anonymous. Yellow pine in the southwest. *For. Irrig.* **1905**, *11*, 120–124.
19. Baker, W.L. Historical forest structure and fire in Sierran mixed-conifer forests reconstructed from General Land Office survey data. *Ecosphere* **2014**, *5*, 79. [CrossRef]
20. Williams, M.A.; Baker, W.L. Testing the accuracy of new methods for reconstructing historical structure of forest landscapes using GLO survey data. *Ecol. Monogr.* **2011**, *8*, 63–88. [CrossRef]
21. Williams, M.A.; Baker, W.L. Bias and error in using survey records for ponderosa pine landscape restoration. *J. Biogeogr.* **2010**, *37*, 707–721. [CrossRef]
22. Baker, W.L. *The Landscapes They are a-Changin': Severe 19th-Century Fires, Spatial Complexity, and Natural Recovery in Historical Landscapes on the Uncompahgre Plateau*; CFRI-1704, Colorado Forest Restoration Institute, Colorado State University: Fort Collins, CO, USA, 2017.
23. Delincé, J. Robust density estimation through distance measurements. *Ecology* **1986**, *67*, 1576–1581. [CrossRef]
24. Baker, W.L. Implications of spatially extensive historical data from surveys for restoring dry forests of Oregon's eastern Cascades. *Ecosphere* **2012**, *3*, 23. [CrossRef]
25. Williams, M.A.; Baker, W.L. High-severity fire corroborated in historical dry forests of the western United States: Response to Fulé et al. *Glob. Ecol. Biogeogr.* **2014**, *23*, 831–835. [CrossRef]
26. Matonis, M.S.; Binkley, D.; Tuten, M.; Cheng, T. *The Forests They Are a-Changin'-Ponderosa Pine and Mixed Conifer Forests on the Uncompahgre Plateau in 1875 and 2010–13*; Colorado Forest Restoration Institute, Colorado State University: Fort Collins, CO, USA, 2014.
27. Woolsey, T.S., Jr. *Western Yellow Pine in Arizona and New Mexico*; USDA Forest Service Bulletin 101, U.S. Government Printing Office: Washington, DC, USA, 1911.
28. Pearson, G.A. The role of aspen in the reforestation of mountain burns in Arizona and New Mexico. *Plant World* **1914**, *17*, 249–260.
29. Margolis, E.Q.; Swetnam, T.W.; Allen, C.D. A stand-replacing fire history in upper montane forests of the southern Rocky Mountains. *Can. J. For. Res.* **2007**, *37*, 2227–2241. [CrossRef]
30. Binkley, D.; Alsanousi, A.; Romme, W.H. Age structure of aspen forests on the Uncompahgre Plateau, Colorado. *Can. J. For. Res.* **2014**, *44*, 836–841. [CrossRef]
31. Brown, H.E. Gambel oak in west-central Colorado. *Ecology* **1958**, *39*, 317–327. [CrossRef]
32. Baker, W.L. *Fire Ecology in Rocky Mountain Landscapes*; Island Press: Washington, DC, USA, 2009.
33. Baker, F.S.; Korstian, C.F. *Suitability of Brush Lands in the Intermountain Region for the Growth of Natural or Planted Western Yellow Pine Forests*; USDA Technical Bulletin No. 256, U.S. Government Printing Office: Washington, DC, USA, 1931.
34. Agee, J.K. *Fire Ecology of Pacific Northwest Forests*; Island Press: Washington, DC, USA, 1993.
35. Baker, W.L. Historical Northern spotted owl habitat and old-growth dry forests maintained by mixed-severity wildfires. *Landsc. Ecol.* **2015**, *30*, 655–666. [CrossRef]

36. Mehl, M.S. Old-growth descriptions for the major forest cover types in the Rocky Mountain region. In *Old-Growth Forests in the Southwest and Rocky Mountain Regions, Proceedings of a Workshop*; Kaufmann, M.R., Moir, W.H., Bassett, R.L., Eds.; USDA Forest Service General Technical Report RM-213; Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO, USA, 1992; pp. 106–120.
37. Popp, J.B.; Jackson, P.D.; Bassett, R.L. Old-growth concepts from habitat type data in the Southwest. In *Old-Growth Forests in the Southwest and Rocky Mountain Regions, Proceedings of a Workshop*; Kaufmann, M.R., Moir, W.H., Bassett, R.L., Eds.; USDA Forest Service General Technical Report RM-213; Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO, USA, 1992; pp. 100–105.
38. Moore, M.M.; Huffman, D.W.; Fulé, P.Z.; Covington, W.W.; Crouse, J.E. Comparison of historical and contemporary forest structure and composition on permanent plots in southwestern ponderosa pine forests. *For. Sci.* **2004**, *50*, 162–176.
39. Farris, C.A.; Baisan, C.H.; Falk, D.A.; Yool, S.R.; Swetnam, T.W. Spatial and temporal corroboration of a fire-scar-based fire history in a frequently burned ponderosa pine forest. *Ecol. Appl.* **2010**, *20*, 1598–1614. [CrossRef] [PubMed]
40. Fulé, P.Z.; Korb, J.E.; Wu, R. Changes in forest structure of a mixed conifer forest, southwestern Colorado, USA. *For. Ecol. Manag.* **2009**, *258*, 1200–1210.
41. Aoki, C.F. Fire History and Serotiny in the Rocky Mountains of Colorado. Master's Thesis, Colorado State University, Fort Collins, CO, USA, 2010.
42. Romme, W.H.; Floyd-Hanna, L.; Hanna, D.O.; Bartlett, E. Aspen's ecological role in the West. In *Sustaining Aspen in Western Landscapes: Symposium Proceedings*; Shepperd, W.D., Binkley, D., Bartos, D.L., Stohlgren, T.J., Eskew, L.G., Eds.; USDA Forest Service Proceedings RMRS-P-18, Rocky Mountain Research Station: Fort Collins, CO, USA, 2001; pp. 243–259.
43. Hanson, C.T.; Sherriff, R.L.; Hutto, R.L.; DellaSala, D.A.; Veblen, T.T.; Baker, W.L. Setting the stage for mixed- and high-severity fire. In *The Ecological Importance of Mixed-Severity Wildfires: Nature's Phoenix*; DellaSala, D.A., Hanson, C.T., Eds.; Elsevier: Amsterdam, The Netherlands, 2015; pp. 3–22.
44. Hessburg, P.F.; Spies, T.A.; Perry, D.A.; Skinner, C.N.; Taylor, A.H.; Brown, P.M.; Stephens, S.L.; Larson, A.J.; Churchill, D.J.; Povak, N.A.; et al. Tamm Review: Management of mixed-severity fire regime forests in Oregon, Washington, and northern California. *For. Ecol. Manag.* **2016**, *366*, 221–250. [CrossRef]
45. Williams, M.A.; Baker, W.L. Comparison of the higher-severity fire regime in historical (A.D. 1800s) and modern (A.D. 1984–2009) montane forests across 624,156 ha of the Colorado Front Range. *Ecosystems* **2012**, *15*, 832–847. [CrossRef]
46. Williams, M.A.; Baker, W.L. Variability of historical forest structure and fire across ponderosa pine landscapes of the Coconino Plateau and south rim of Grand Canyon National Park, Arizona, USA. *Landsc. Ecol.* **2013**, *28*, 297–310. [CrossRef]
47. Baker, W.L. Are high-severity fires burning at much higher rates recently than historically in dry-forest landscapes of the western USA? *PLoS ONE* **2015**, *10*, e0136147.
48. Sherriff, R.L.; Platt, R.V.; Veblen, T.T.; Schoennagel, T.L.; Gartner, M.H. Historical, observed, and modeled wildfire severity in montane forests of the Colorado Front Range. *PLoS ONE* **2014**, *9*, e106971. [CrossRef]
49. Tepley, A.J.; Veblen, T.T. Spatiotemporal fire dynamics in mixed-conifer and aspen forests in the San Juan Mountains of southwestern Colorado, USA. *Ecol. Monogr.* **2015**, *85*, 583–603. [CrossRef]
50. Kulakowski, D.; Veblen, T.T.; Drinkwater, S. The persistence of quaking aspen (*Populus tremuloides*) in the Grand Mesa area, Colorado. *Ecol. Appl.* **2004**, *14*, 1603–1614. [CrossRef]
51. Veblen, T.T.; Kitzberger, T.; Donnegan, J. Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. *Ecol. Appl.* **2000**, *10*, 1178–1195. [CrossRef]
52. DeBuys, W.; Allen, C.D. A historical chronology of events and observations for the Pecos Wilderness in the Territorial period. *N. M. Hist. Rev.* **2015**, *90*, 415–487.
53. Morrow, R.J. Age Structure and Spatial Pattern of Old-Growth Ponderosa Pine in Pringle Falls Experimental Forest, Central Oregon. Master's Thesis, Oregon State University, Corvallis, OR, USA, 1986.
54. DellaSala, D.A.; Hanson, C.T. (Eds.) *The Ecological Importance of Mixed-Severity Fires, Nature's Phoenix*; Elsevier: Amsterdam, The Netherlands, 2015.
55. Baker, W.L. Transitioning western U.S. dry forests to limited committed warming with bet-hedging and natural disturbances. *Ecosphere* **2018**, *9*, e02288. [CrossRef]

56. Wu, R. Fire History and Forest Structure in the Mixed Conifer Forests of Southwest Colorado. Master's Thesis, Colorado State University, Fort Collins, CO, USA, 1999.
57. Baker, W.L.; Williams, M.A. Bet-hedging dry-forest resilience to climate-change threats in the western USA based on historical forest structure. *Front. Ecol. Evol.* **2015**, *2*, 88. [CrossRef]
58. Dugan, A.J.; Baker, W.L. Sequentially contingent fires, droughts, and pluvials structured a historical dry forest landscape and suggest future contingencies. *J. Veg. Sci.* **2015**, *26*, 697–710. [CrossRef]
59. Romme, W.H.; Jamieson, D.W.; Redders, J.S.; Bigsby, G.; Lindsey, J.P.; Kendall, D.; Cowen, R.; Kreykes, T.; Spencer, A.W.; Ortega, J.C. Old-growth forests of the San Juan National Forest in southwestern Colorado. In *Old-Growth Forests in the Southwest and Rocky Mountain Regions, Proceedings of a Workshop*; Kaufmann, M.R., Moir, W.H., Bassett, R.L., Eds.; USDA Forest Service General Technical Report RM-213; Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO, USA, 1992; pp. 154–165.
60. Swanson, M.E.; Franklin, J.F.; Beschta, R.L.; Crisafulli, C.M.; DellaSala, D.A.; Hutto, R.L.; Lindenmayer, D.B.; Swanson, F.J. The forgotten stage of forest succession: Early-successional ecosystems on forest sites. *Front. Ecol. Environ.* **2011**, *9*, 117–125. [CrossRef]
61. Battaglia, M.A.; Gannon, B.; Brown, P.M.; Fornwalt, P.J.; Cheng, A.S.; Huckaby, L.S. Changes in forest structure since 1860 in ponderosa pine dominated forests in the Colorado and Wyoming Front Range, USA. *For. Ecol. Manag.* **2018**, *422*, 147–160. [CrossRef]
62. Schoennagel, T.; Balch, J.K.; Brenkert-Smith, H.; Dennison, P.E.; Harvey, B.J.; Krawchuk, M.A.; Mietkiewicz, N.; Morgan, P.; Moritz, M.A.; Rasker, R.; et al. Adapt to more wildfire in western North American forests as climate changes. *Proc. Nat. Acad. Sci. USA* **2017**, *114*, 4582–4590. [CrossRef]
63. McWethy, D.B.; Schoennagel, T.; Higuera, P.E.; Krawchuk, M.; Harvey, B.J.; Metcalf, E.C.; Schulz, C.; Miller, C.; Metcalf, A.L.; Buma, B.; et al. Rethinking resilience to wildfire. *Nat. Sustain.* **2019**, in press. [CrossRef]
64. Graham, R.T.; Asherin, L.A.; Battaglia, M.A.; Jain, T.B.; Mata, S.A. *Mountain Pine Beetles: A Century of Knowledge, Control Attempts, and Impacts Central to the Black Hills*; USDA Forest Service General Technical Report RMRS-GTR-353; Rocky Mountain Research Station: Fort Collins, CO, USA, 2016.