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Envisioning Transition from Open Landscapes to Forested Landscapes in the Routt National Forest, Colorado, United States

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Abstract: Globally, in remaining wildlands, tree densities and forested cover have increased in grasslands and open forests since European settlement. In the southern Rocky Mountains of Colorado, United States, we determined tree composition and tree cover from historical (years 1875 to 1896) surveys and compared them to current (2002 to 2011) tree composition and current (year 2016) forested land cover for 500,000 ha of the Routt National Forest. Additionally, we examined whether changes in precipitation occurred. Regarding composition, pine (primarily lodgepole pine; *Pinus contorta*) decreased from 65% to 32% of all trees, with increased subalpine fir (*Abies lasiocarpa*) from 0.5% to 23% of all trees, and quaking aspen (*Populus tremuloides*) from 13% to 30% of all trees. According to 80% of 5175 survey points not in forests, the historical landscape was very open, comprised of grasslands, mountain meadows, and other open ecosystems. In contrast, 75% of the current landscape is covered by forests. Change points in the Palmer Modified Drought Index were within historical limits, indicating that forestation was not related to a change in water availability. Based on historical surveys and accounts, we envisioned a historical landscape that was open but embedded with dense lodgepole pine clusters and spruce stands at high elevations, which has now become a predominantly forested landscape of dense forests, similar to global forestation patterns.

Keywords: colonization; expansion; forestation; historical; lodgepole pine; quaking aspen; settlement; subalpine fir

Citation: Hanberry, B.B.; Seidel, J.M. Envisioning Transition from Open Landscapes to Forested Landscapes in the Routt National Forest, Colorado, United States. *Fire* **2024**, *7*, 82. https://doi.org/10.3390/fire7030082

Academic Editor: Panteleimon Xofis

Received: 28 January 2024
Revised: 26 February 2024
Accepted: 5 March 2024
Published: 6 March 2024

1. Introduction

Although deforestation is one land use trajectory, another trajectory due to land use disturbance is afforestation and increased tree densities in wildlands, forcing the transition of grasslands or open forests of savannas and woodlands to forests comprised of dense tree growth. A sequence of fire exclusion and replacement of grasslands and open forests, which were typically managed by Indigenous peoples with burning, by forestation following European settlement has been documented in Australia [1,2], southern Africa [1], southern Asia [3,4], South America [1], probably throughout Eurasia [5], and North America [6–8]. As a general rule, changes within forests during the past century in the United States include increased tree density, particularly in the abundance and diversity of fire-sensitive species, and fuel accumulation, critically of surface and ladder tree fuels [9,10]. Equally, trees have invaded grasslands, resulting in afforestation [11]. Forestation, whether afforestation in open ecosystems or tree densification in forests, results in biodiversity and habitat loss and may increase the severity of fire, damage from insect outbreaks, use of water, and vulnerability to climate change [7,9,10,12–16].

Historical ecosystems were documented methodically but not specifically quantified in most early historical assessments of the western United States. Forests were not continuous or dense in the southern Rocky Mountains of Colorado and Wyoming [17]. In Colorado, Ensign [18] and Gannett [17] described forests as irregular masses confined to high mountains and plateaus, separated by wide spaces. Sudworth [19] stated: “The timbered areas. . .share, in their character, the common feature of the entire Rocky Mountain region, in rarely consisting of extensive bodies of forest growth." Trees occurred as single trees or disconnected groups and groves of trees at lower elevations, with more continuous cover at high elevations, above 2750 m, particularly on northern slopes [19]. Most of the southern Rocky Mountains were grasslands of parks and mountain meadows [19,20]. Herbaceous species may have been primarily representative of the Great Plains grasslands excepting at elevations of subalpine and alpine zones [21–23]. Trees likewise were rare in the foothills, which consisted of grasslands, brushlands (i.e., comprised of shrubby trees including *Quercus gambelii*), and sagebrush shrublands (*Artemisia*; [19,20]). Contrary to contemporaneous assessments, research overall conveys the southern Rocky Mountains as forested [24].

Euro-American settlement resulted in extensive and intensive land use changes, including logging, grazing by domestic livestock, and fire exclusion [25]. The United States acquired Colorado and Wyoming east of the Continental Divide, in the Rocky Mountains, during 1803 and the rest of Colorado and Wyoming during 1848, with cattle ranchers as early inhabitants [25]. The Overland Trail and the first transcontinental railroad, completed during 1869, transported Euro-American settlers through southern Wyoming (Figure 1; [25]). The discovery of gold and other mineral resources in Colorado brought an influx of Euro-American settlers starting in 1858, concentrated in the Front Range region, or the eastern side of the southern Rocky Mountains, along a mineral resource band that extended to southwestern Colorado, and in southern Wyoming (Figure 1; [18,26]). Between 1860 and 1880, the Euro-American population of Colorado increased from 25,000 to 200,000, which then doubled to 400,000 by 1890 [26]. The harvest of forest products occurred in accessible, lower-elevation sites that were within a day (or about 16 km) of local markets or railroad stations [20].

Land use changed the frequency and severity of fires, which influenced ecosystem types [9]. In general, high elevations of cold, protected locations experienced infrequent, high-severity fires after the accumulation of coarse tree fuels, whereas lower elevations experienced frequent surface fires fueled by herbaceous vegetation [10]. Different fire regimes filter species by response traits, and the montane and subalpine tree species of lodgepole pine (*Pinus contorta*), quaking aspen (*Populus tremuloides*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) respond well to stand-replacing disturbances through reproduction and stand initiation, but, typically, small-diameter trees of these species do not survive to compete against fire-tolerant tree, shrub, and herbaceous species under frequent surface fires [27,28]. Surface fire-tolerant ponderosa pine and Douglas-fir are common in montane, lower-elevation woodlands on the eastern side of the southern Rocky Mountains, but not the western side [19,20,29]. Fires were frequent historically in the region, and fire frequencies appeared to increase with initial Euro-American activities during the late 1800s [19,20,24,29]. During the early 1900s, fire exclusion became standard management to prevent forest destruction and the waste of valuable forest products, leading to disruptions in the natural fire cycle of many ecosystems [30]. In southern Wyoming, few and small fires occurred after forest reserves, precursors to National Forests, were established as early as 1902 [31,32]. Fire reconstructions for subalpine forests in the region indicated fire return intervals every 135 to 300 years, based on charcoal, which aligned well with an estimated fire rotation of 125 to 170 years for stand-replacing events equal to the area of the study extent (3250 ha) for a fire scar study, but with a composite mean fire interval of 5.5 to 8.4 years and point-scale mean fire interval of 39 to 149 years [33,34]. Thus, by some fire reconstruction measures, which have issues both in terms of detection and methods [35–38], fire exclusion since the early 1900s may not yet be a departure from historical fire regimes in high-elevation subalpine forests.

Slight forest cover increases have been documented in the southern Rocky Mountains of Colorado and Wyoming since Euro-American settlement. Using aerial imagery, Rodman et al. [39] found that forest cover in northern Colorado increased by 8% between 1938 and 2015. For the same region during 1938–1999, Platt and Schoennagel [40] detected a 4% increase in forest cover, with no increases in forest cover above 2432 m. In Wyoming, 7% of historical openings within forests were lost to tree invasion from 1883 to 1994 based on the reconstruction of forests openings from notes in the original General Land Office (GLO) surveys compared to modern forest openings interpreted from digital aerial photography [41].

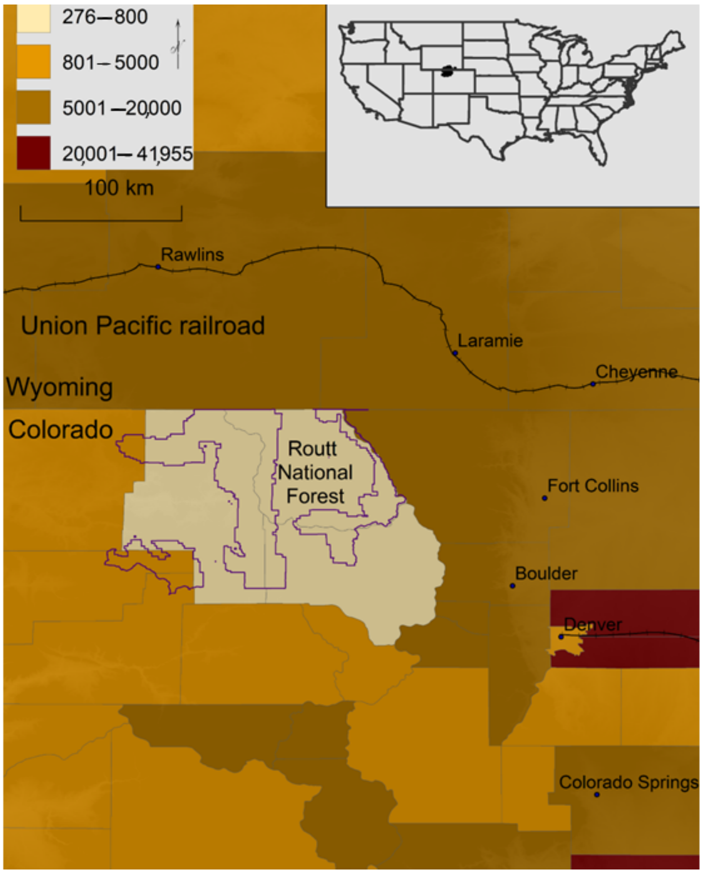

Figure 1. Population per county [26] remained low (≤800) during 1890, with limited infrastructure, in the Routt National Forest, Colorado, while transportation networks and gold and other mineral resources concentrated Euro-American settlers in the Front Range region, or the eastern side of the southern Rocky Mountains, and southern Wyoming.

Even though structure may not be expected to change within forests that experienced infrequent fire, the expansion of trees and establishment of new forests may occur in mountain meadows and lower-elevation open ecosystems of treeless river valleys, grasslands, and shrublands, due to fire exclusion and disturbance change associated with Euro-American settlement. In Colorado, the Routt National Forest may have resembled the White River Plateau Reserve on the southern border, which did not have any large, continuous bodies of timber, excepting a few watersheds, and instead contained single trees, groves, and small stands interspersed within grassy parks [19]. To explore potential tree expansion, and of which species, we determined tree composition and tree cover recorded in General Land Office surveys conducted during the years of 1875 to 1896 for about 500,000 ha of the Routt National Forest, which remained relatively inaccessible and undisturbed by intensive and extensive timber harvest during this interval (Figures 1 and 2). We compared historical tree composition to composition from modern surveys of the USDA Forest Service Forest Inventory and Analysis (FIA; [42,43]) and historical tree cover to forest cover from the 2016 National Land Cover Database (NLCD; [44]). We generally outlined a potential core area of expansion where trees were not recorded at historical survey points but where current land cover was forested. Although fire exclusion is one reason for tree expansion immediately following Euro-American settlement, increased precipitation is attributed as another reason for tree establishment in climates where water is limited [45,46]. Therefore, we also assessed the Palmer Modified Drought Index (PMDI), which is modeled from tree-ring chronologies and calibrated and validated with instrumental data [47] as a proxy for available water to determine if sustained changes in mean values have occurred since 1900 compared to previous centuries [11]. Formally, we asked how has tree composition and forest cover changed in the Routt National Forest between 1875 and 1896 to near present day and is there a correlation with increased water availability for trees?

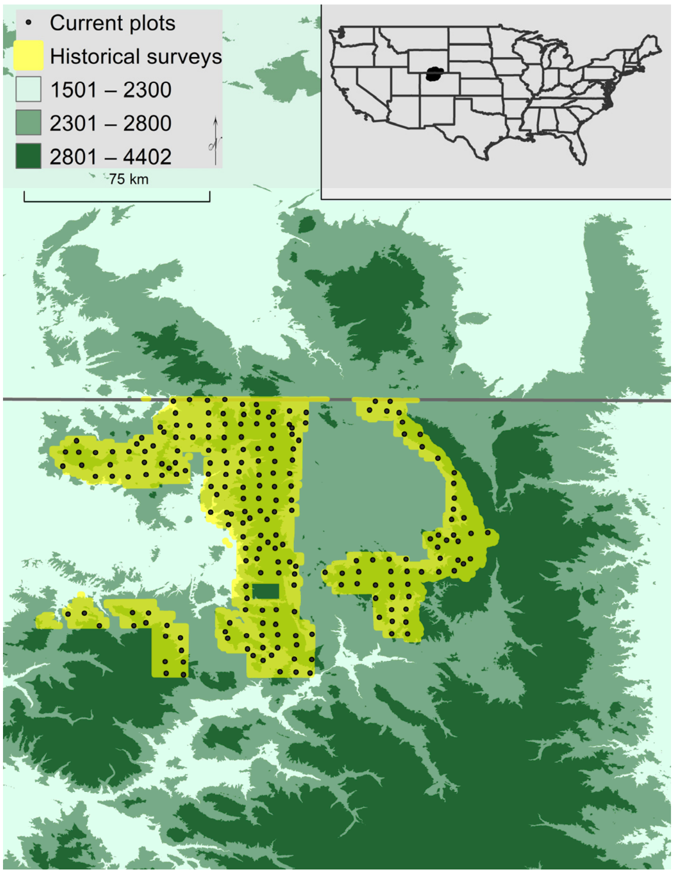

Figure 2. The Medicine Bow and Routt National Forests, Colorado and Wyoming, are in the southern Rocky Mountains. The study extent was the area with available records of General Land Office tree surveys in the Routt National Forest, Colorado (square yellow sections encompassing 5175 survey points), which contained the approximate locations of current Forest Inventory and Analysis plots (black points).

2. Materials and Methods

2.1. Tree Surveys and Comparison of Composition over Time

The General Land Office, created during 1812, developed and directed surveys of the Public Land Survey System of townships and ranges based on 1.6 km square sections (Figure 3; [48]). Surveyors recorded the species, diameter, distance, and bearing of two to four trees in a point-centered quarter method every 0.8 km at the corners and middle of each section line. Generally, for section lines within townships, surveyors started surveying at the southeastern-most section line. If trees were not present within 60 m, surveyors were instructed to set a stone, mound, or post to record the location.

We transcribed 5175 survey points from 93 townships that intersected with the Routt National Forest in Colorado (Figure 2) from scanned General Land Office field notes [49]. The survey points, surveyed between 1875 and 1896, represented 2991 trees with diameters $\geq$ 12.7 cm at 1.37 m height, after excluding about 100 trees that had diameters < 12.7 cm. However, 3605 survey points (70%) had no trees recorded due to distances to nearest trees exceeding 60 m. An additional 452 points (9%) had only one tree recorded, indicating that a second tree was greater than 60 m in distance, which translates into tree densities representative of grasslands. About 40 points were irregular, such as survey points at rocks or water bodies or with trees recorded that did not meet moderate diameter standards, with diameters < 12.7 cm [48].

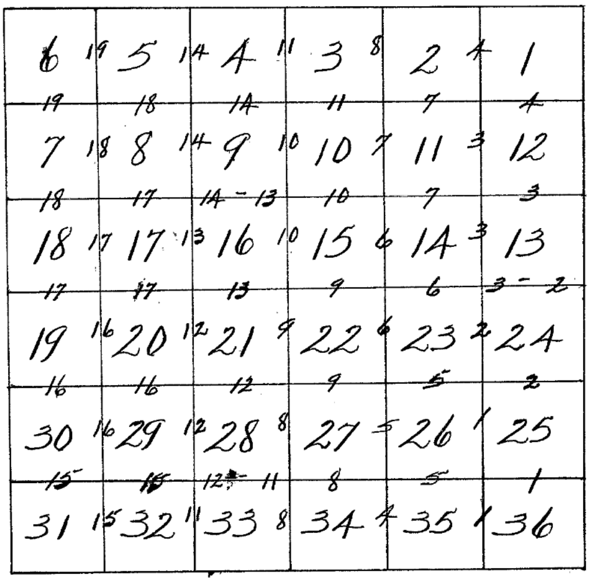

Figure 3. Example of an index map for surveys of 36 (numbered in center) square sections, with survey points at the section corners and middle of section lines indicated by additional numbers, which are the corresponding page numbers that contain the survey point information.

The USDA Forest Service Forest Inventory and Analysis [42] has long-term forest plots, consisting of four 7.31 m radius subplots, configured as a central subplot surrounded by three outer subplots [43]. Plots are sited about every 2500 ha and are typically visited every five to ten years. We extracted 220 plots with coordinates within the extent of the available sections with historical surveys. True plot coordinates are not available because of a privacy provision in the Food Security Act of 1985 [50]. Plot coordinates are within 1.6 km of the true locations, and most plots are within 0.8 km, and plot coordinates on private lands also are exchanged for up to 20% of plots. We selected a complete cycle of surveys from the years 2002 to 2011, representing 8463 trees with diameters ≥12.7 cm at 1.37 m height.

From these datasets, we quantified the composition, or percent of all trees, for each species or genera. For historical surveys, surveyors overall did not differentiate species, and generally, locations do not provide enough information to identify species [8]. Spruces included Douglas-fir because Douglas spruce was in common use during this time interval [19,20], and also as evidenced from a letter written by John Muir, famed naturalist, to Charles Sprague Sargent, the first director of Harvard's Arnold Arboretum and author of the first census of forests nationally [51]. Historical accounts and modern surveys can assist with the identification of tree species.

We calculated mean and maximum diameters for each species. Surveyors selected trees of medium diameter that were sound, with few trees below diameters ≥ 12.7 cm at 1.37 m height [48]. We recognize that the historical distribution of trees may have contained a greater percentage of larger trees (see results about diameters) due to limited locations of frequent overstory disturbance relative to extensive and intensive harvesting following Euro-American land use changes (see Introduction and Discussion sections). Trees <12.7 cm also are sampled less intensively in modern surveys, and we compared truncated (≥12.7 cm) samples [43].

2.2. Comparison of Land Cover over Time

The historical study extent had 80% of 5175 systematic survey points with no or only one tree, where the surveyor set a stone as a marker. Any survey points without recorded trees had extremely low densities, at about 1 tree/ha (i.e., estimated density where distances of 60 m). Survey points with only one recorded tree less than 60 m also have tree densities representative of grasslands.

Because of the predominantly open nature of the historical surveys, the best comparison to current conditions may be land cover. Land cover is not possible to extract from FIA plots, which only occur in forests and have few samples, namely 220 plots at one per 2500 ha (Figure 1). We used the 2016 National Land Cover Database [44]. The resolution is 30 m, and forests are classified by tree cover greater than 20% of total vegetation cover. We clipped the land cover to the study extent and then calculated percentage forested cover, excluding perennial snow cover, open water, and developed land covers.

2.3. Identification of Potential Core Area of Expansion

We estimated a potential core area of expansion for a contiguous area that was historically unforested (i.e., survey points without recorded trees) and currently forested. Surveys occurred along section lines, but we located sections that contained more historical survey points without trees than survey points with trees along the west and north boundary lines. Then, we retained contiguous sections that formed a core area, removing isolated sections. To identify expansion, we clipped the core area to intersect with current forest land cover. That is, the potential core area of expansion delineated change from contiguous sections predominantly without trees (i.e., either two or three survey points without trees for three points in a section) historically to current forest cover. Then, we determined elevational differences in the potential core area of expansion relative to outside the potential core area of expansion and if any particular species were currently more abundant within the potential core area of expansion than outside the potential core area of expansion.

2.4. Influence of Water Availability

Varying moisture availability is often offered as an explanation for changes in tree densities and distributions in the late 1800s and early 1900s [45,46]. Precipitation alone does not account for water balance. The Palmer Modified Drought Index (PMDI), modeled from tree-ring chronologies calibrated with instrumental data [47], may be the most accurate proxy of available water for trees over time. The PMDI values range from −5 to 5, with drought severity represented by negative numbers. Reconstructions extend PMDI estimates to over 2000 years on a 0.5-degree grid.

Sequential change point detection applies statistical tests to identify points of change in the properties of a time series. A variety of different approaches to identify change point detection are available because one method may not identify all major change points efficiently. Therefore, to detect major change points since year 0, two methods were used for change points that applied different algorithms and options: changepoint package with the PELT algorithm and cpm package with *t*-test [52–54]. If unparalleled ecological changes occurred, then we would expect both change point approaches to detect sustained changes in precipitation outside of the historical range of variation that was initiated during the late 1800s.

3. Results

For composition, pine (primarily lodgepole pine, based on historical accounts and modern surveys) decreased from 65% to 32% of all trees, due to increases in subalpine fir and quaking aspen (Table 1). Subalpine fir increased from 0.5% to 23% of all trees, and quaking aspen increased from 13% to 30% of all trees. Pine, spruces (that is, primarily *Picea engelmannii* with minor *Pseudotsuga menziesii*), and aspen were the only historical genera with relatively good sample sizes. Pine (27.1 cm) and spruce (28.2 cm) had larger diameters historically than in modern surveys, which had mean diameters of 21 cm for pine and spruce. Conversely, aspen diameters increased slightly, with smaller historical diameters that match with historical accounts of suppressed aspen trees.

Table 1. Composition and diameter of trees (diameters ≥ 12.7 cm at 1.37 m height) for historical (years 1875 to 1896) and current (years 2002 to 2011) surveys in the Routt National Forest, Colorado.

		Composition		Diameter (cm)	
Scientific Name	**Common Name**	**Count**	**Percent**	**Mean**	**Max**
Historical (common names similar to survey entries)					
Pinus contorta	pine	1949	65.1	27.1	76.2
Picea engelmannii, *Pseudotsuga menziesii*	spruce	630	21.1	28.2	76.2
Populus tremuloides	aspen	394	13.2	20.2	50.8
Abies lasiocarpa	fir	9	0.3	25.1	40.6
Populus deltoides, *angustifolia*	cottonwood	5	0.2	22.4	30.5
Quercus gambelii	oak	4	0.1	18.4	33
Current					
Pinus contorta	lodgepole pine	1837	31.7	21.1	52.8
Populus tremuloides	quaking aspen	1727	29.8	21.1	53.6
Abies lasiocarpa	subalpine fir	1336	23.0	21	81.3
Picea engelmannii	Engelmann spruce	726	12.5	25.2	84.6
Pseudotsuga menziesii	Douglas-fir	131	2.3	23.5	77.5
Quercus gambelii	Gambel oak	18	0.3	16.6	27.7
Abies lasiocarpa var. *arizonica*	corkbark fir	13	0.2	17.7	31
Picea pungens	blue spruce	11	0.2	32.5	57.7

Only about 20% of the historical survey points even qualified as possible to be inside forest locations, in that two trees were located within 60 m, but some of these survey points may have been located outside of forest cover. The number of survey points (about 80%) without two trees within 60 m signified that the landscape was very open, or generally representing grasslands of mountain meadows and parks. Currently, 75% of the study extent, or 383,000 ha, consisted of forested vegetation cover, defined by tree cover greater than 20% of total vegetation within 30 m cells.

Regarding the potential core area of expansion, the predominantly historical treeless contiguous area with current forest cover covered approximately 257,000 hectares of the 475,000 ha study extent (Figure 4; excluding irregular Public Land Survey System units such as 'unsurveyed unprotracted'). Sections that were predominantly treed historically had a mean elevation of 2820 m, and sections that were predominantly not treed historically had a mean elevation of 2840 m. Current tree cover occurred at a mean elevation of 2805 m inside the potential core area of expansion and 2845 m outside of the potential core area of expansion, similar to mean elevations of current forest plot locations at 2805 m inside and 2835 m outside the potential core area of expansion. That is, the potential core area of expansion was at lower elevations than the non-expansion area with trees. Thus, potential forest expansion may have been slightly downslope overall to lower elevations. Currently, the potential core area of expansion had more spruce and less lodgepole pine compared to outside the potential core area of expansion.

For the Palmer Modified Drought Index (PMDI; Figure 5), a proxy of water availability for trees, change points after the year 1500 occurred only for one change point approach during the years 1827, 1845, 1905, 1933, and 1982 in the Routt National Forest. Although these were statistically significant change points, the mean PMDI values did not display any precipitation extremes, as mean values between change points ranged from -0.35 to 1.1 on a -5 to 5 scale: 0.06 during 1500 to 1826, 1.1 during 1827 to 1844, -0.35 during 1845 to 1904, 0.96 during 1905 to 1932, and 0.0 between 1933 and 1982. Surveys and historical accounts specified a very open landscape during the years 1875 to 1896. The PMDI values during 1905 to 1932, during the initial interval of landscape change, were not outside the range of historical variation for historical forests as they were encompassed by the values during 1827 to 1844, before the interval of landscape change, and different decadal intervals during 1500 to 1826. The other change point approach did not identify change points after the year 1200.

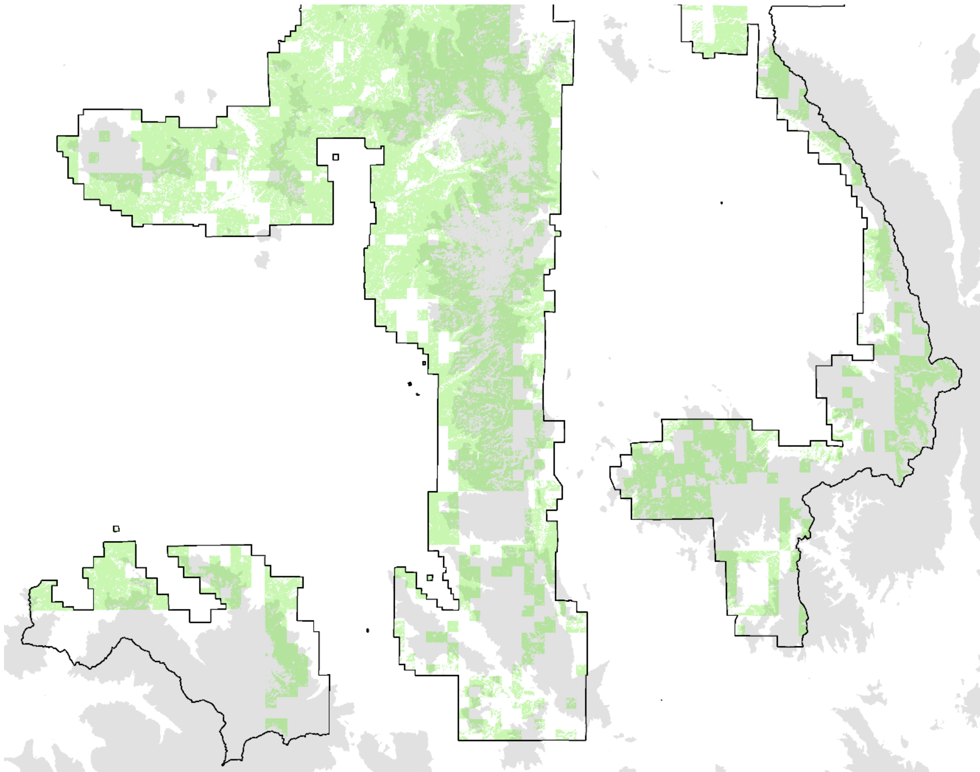

Figure 4. Potential core area of expansion (green), where historical surveys predominantly did not have trees and current cover was forested compared to elevation >2800 m (gray).

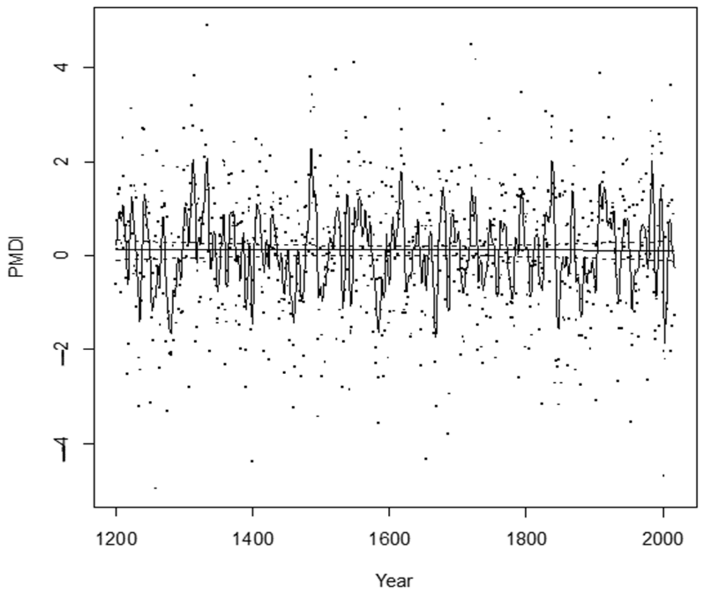

Figure 5. Palmer Modified Drought Index (PMDI; annual value points with fitted line, slope, and 95% confidence interval) during years 1200 to 2017 for the Routt National Forest. The Palmer Modified Drought Index, modeled from tree-ring chronologies and instrumental data [47], is a proxy of available water for trees over time. Drought intensity is represented by negative numbers.

4. Discussion

4.1. Transition to a Forested Landscape

Tree expansion outside of forests and increased tree densities within forests are outcomes of fire exclusion associated with European colonization in the western United States and globally [1–6,8–10]. In the Routt National Forest, southern Rocky Mountains, Colorado, a reversal occurred from an open historical (1875 to 1896) landscape to a forested current landscape (2002 to 2016). These findings are based on 80% of 5175 systematic survey points not in forests historically compared to 75% of the entire study extent currently classified as forested cover. Although the historical surveys offer a systematic assessment of tree presence at landscape scales, the historical extent of open landscapes was not possible to clearly define based on survey points. That is, some of the 20% of survey points with two recorded trees within 60 m may have been located outside of forest cover, but within 60 m of trees; conversely, 80% of survey points not in forests may not convert directly to 80% of the historical landscape containing comprehensive open ecosystem cover. Although samples do not provide complete coverage, the contiguous area that was predominantly comprised of sections with treeless survey points historically covered about 75% of the landscape. Forests currently occur in part of this historical contiguous treeless area, resulting in a potential core area of expansion that is about 55% of the landscape. Additionally, with survey points, it was not possible to isolate tree expansion dynamics. Nonetheless, the expansion of tree cover downslope to lower elevations overall appeared to occur. While the potential core area of expansion is represented by spruce currently, early researchers noted the initial expansion of lodgepole pine, particularly downslope [21,55]. Trees in afforested areas particularly may be vulnerable to drought, climate change, and associated disturbances [13].

The historical tree surveys combined with historical accounts illustrated the intermixing of primarily non-treed ecosystems with lodgepole pine clusters and Engelmann spruce stands, which may have occurred only densely on north and west slopes at high elevations [17,19,20]. Lodgepole pine and Engelmann spruce, the predominant historical species, are not known now for occurring in low-density woodlands, under low-severity surface fire regimes that control tree densities. Lodgepole pine and Engelmann spruce do not have traits, such as thick bark development in young trees, to survive frequent surface fires; rather, they typically re-establish rapidly at high densities after severe disturbance, promulgating future dense stands. The greater tree densities found on spruce stands at northern high-elevation slopes, according to historical accounts, likely indicated that these sites were most protected from fires, while lower-elevation lodgepole pine clusters escaped frequent surface fire in fine-scale firebreaks, such as topographic irregularities, boulders, and fallen logs. Mason [56] noted that grass fires invariably occurred and spread over large areas, resulting in damage to lodgepole pines. Likewise, Hayden [57] described numerous fires that spread up mountain sides from open mountain parks and treeless river valleys, resulting in burned timber. Given limited extents of forests, fire largely may be confined to herbaceous plants and shrubs, resulting in short flame lengths and low-severity surface fires, as defined by limited mortality to canopy trees [24]. When surface fires encountered dense lodgepole pine clusters, these trees may have torched but were surrounded by vegetation that did not have the vertical fuel to accommodate high-severity fires. When surface fires encountered larger spruce stands on northern slopes, high-severity fires may have occurred, particularly under dry, windy conditions of extreme fire weather [58]. Otherwise, the surface fires may have extinguished when encountering the coarse tree fuels and more protected conditions of forest stands, but south slopes were likely more exposed and dry, allowing fires to spread up in elevation.

It is possible that the open landscape was partially due to selective harvesting during the survey interval of 1875 to 1896. However, during this interval, the study extent remained inaccessible from markets of population centers and major railroad lines (Figure 1), compared to the lower-elevation forests of southern Wyoming, which were being harvested for railroad ties, and the lower-elevation forests on the eastern side of the Continental Divide in Colorado, which were being harvested for lumber with portable sawmills [19,20,31]. Even within regions where selective harvest occurred, Hayden [57], Ensign [18], Jack [20], and Sudworth [19] described primarily open landscapes.

We found that the transition from an open to closed landscape in the Routt National Forest was more severe than the 4% to 8% increase in tree cover detected in other studies for the region since 1938 [39,40], although results corresponded with general increased tree expansion throughout the United States [11]. Tree increases likely ensued before 1938, the start date of comparison in photographic studies, particularly because the other study locations became accessible for intensive land use change before the Routt National Forest. Additionally, the other study extents may have encompassed a greater initial proportion of forests, that is, the starting point may have been a forested landscape. While a few decades may not seem like a long enough interval to change the landscape, grasslands have been documented to transition to forests within this time interval [59,60].

Indeed, increased tree establishment initiated before 1920 [58]. Without the mortality of small-diameter trees by fire, trees were able to develop into stands, successfully escaping the fire trap of mortality to small-diameter trees. For example, Mason [61] and Bates [55], early foresters for the USDA Forest Service, noted recent extensive lodgepole pine stands, which originated after fire and survived in the absence of fire. Mason [61] wrote: 'Most of the extensive lodgepole stands now in existence have come in as a result of fire. On the other hand, areas formerly covered with lodgepole have been made barren by "double burns", where stands of young growth which followed the first fire have been destroyed by a second one before they were old enough to produce seed'. Bates [55] stated: 'over large areas the mature lodgepole pine stands which we now possess represent the first generation of the species as a forest dominant in this region'. Similar to lodgepole pine, Engelmann spruce establishes rapidly after fire, given sufficient numbers of seed trees (i.e., in high-elevation areas where Engelmann spruce was abundant; [28]).

Tree composition has shifted in time, with increases in subalpine fir and quaking aspen, which were rarely dominant in historical accounts [20,21]. Despite extensive new stands of lodgepole pine [61], lodgepole pine may no longer have been an extremely dominant tree species by 1915 [56]. All tree species are released to grow without fire mortality, and contemporaneous researchers expected that due to fire exclusion, lodgepole pine would be replaced by Engelmann spruce and Douglas-fir [21,55,61]. Subalpine fir was associated with dominant spruce in the past, but historical disturbance conditions apparently were not conducive to subalpine fir. Subalpine fir does not respond well to large-scale disturbances or compete well against Engelmann spruce and lodgepole pine that initiate rapidly after fires [19,27]. Quaking aspen was widespread throughout all elevations but suppressed, sometimes into a shrubby, low-statured form [19,20]. Quaking aspen regeneration, via sprouts, is favored under mechanical disturbances from logging [62,63]. Quaking aspen may be the beneficiary of exploitative logging of lodgepole pine [62] and recent mountain pine beetle (*Dendroctonus ponderosae*) and spruce beetle (*Dendroctonus rufipennis*) outbreaks that have opened canopies and reduced competition from lodgepole pine and spruce [64].

4.2. Influencing Factors

One reason attributed for the change in tree species distributions and densities following Euro-American settlement is increased precipitation [21,45]. However, the Palmer Modified Drought Index during the 1800s and 1900s remained within the range of previous centuries for this region, without initiation of sustained PMDI values of unusual magnitude. Multidecadal trends were not prominent in this region during the 1900s [24]. That being the case, the increasing species of quaking aspen and subalpine fir share the requirement for moisture, perhaps indicating a response to change in moisture regime, but the decreasing species of Engelmann spruce is only slightly more drought-tolerant than subalpine fir [65]. Increased tree recruitment has been documented to occur during fire-free intervals, regardless of precipitation, during both droughts and pluvials [66,67]. That is, fire-free intervals have a stronger influence than greater precipitation on successful tree recruitment, albeit climate modulates the fuels for fires [67].

The consistent reason for changes in species distributions and abundances, including tree densities, across the U.S. and globally during the last few centuries has been land use change, a component of which is altered fire regimes, following European settlement [1–8,68]. Fire exclusion did occur in the Routt National Forest [25], which is a mechanism that enables small-diameter trees to survive, when previously, fire likely would have killed the vulnerable young trees. Over a century has occurred with limited fire within the Routt National Forest, according to historical accounts of fire cessation during the establishment of forest reserves and fire records since 1945 [25]. In this region, heavy cattle grazing during the end of the 1800s and early 1900s reduced the herbaceous fuels necessary for surface fires and opened growing space for tree establishment [20,25]. The development of roads to access forest resources also stopped surface fire spread. These land use changes tend to be the major requirement to end frequent surface fires and allow for the rapid spread of tree growth, but additionally, the cultural change from active burning to active fire suppression also contributes to surface fire exclusion [11].

Besides fire exclusion, the other understory disturbance of large native herbivores that consume young trees were either extirpated or reached population lows [25], while overgrazing of herbaceous plants by sheep and cattle may have favored small tree establishment. In southern Wyoming, native herbivores of elk (*Cervus canadensis*), deer (*Odocoileus hemionus*), and bighorn sheep (*Ovis canadensis*) were overhunted between 1880 and 1910, leading to extirpation [25]. Sheep and cattle were abundant after about 1870, with grassland overuse apparent by 1890, resulting in pressure on high-elevation mountain valleys [25]. Forage consumption likely reduced the frequency of grassland fires. The sequence of events of large herbivores that occurred in southern Wyoming probably also occurred in the Routt National Forest, but this was delayed due to relative inaccessibility. This progression also occurred throughout the eastern U.S. and globally (e.g., [69]).

Overstory disturbance through the harvest of lodgepole pine and spruce, including the switch to clearcutting, combined with fire exclusion and the extirpation of large native browsers may have removed the influences of thousands of years that favored already established vegetation, the legacy lock or inertia, and rebalanced the tree species to relatively equal proportions of lodgepole pine, aspen, spruce, and fir. In southern Wyoming, the Medicine Bow National Forest, which initially was established as forest reserves during the first decade of the 1900s, selective removal of up to 45% of stands along with the piling and burning of slash occurred until 1935, when harvests of 65–85% of the trees in a stand became common [25]. After 1922, contracts called for the removal of older sawlog trees too large for railroad ties. Strip cutting and dispersed clearcuts practices became common during the late 1940s to maximize wood production in the replacement of slow-growing old forests, re-set high-graded forests, and reduce blowdown in thinned stands, as lodgepole pine was subject to windfall [25]. Without the presence of large overstory trees to control the growing space, resources become available for a high density of small-diameter trees to establish. Roads built after 1950 increased access to subalpine forests, some of which were cut for the first time [25].

Some evidence suggests that in mid- and higher-elevation forests, fires were historically infrequent because of relatively cold and wet conditions, and fire exclusion has not affected forests [70]. However, both charcoal and fire scar studies have issues [35–38], particularly if located in newly expanded forests. Conversely, historical accounts and these land surveys indicated sparse tree cover in the past, with these tree species that auto-replace under severe disturbance clustered in stands embedded in an open landscape [20]. Due to strong winds and adjacency to mountain meadows, grasslands, brushlands, and shrublands at all elevations, surface fire did spread to some extent in lodgepole pine clusters and spruce stands, reducing tree densities [19,57]. Equally, wind-driven fires kept colonizing lodgepole, spruce, and fir species and suppressed aspen from establishing in grasslands [19,57].

5. Conclusions

A transition from an open to a closed landscape occurred in the Routt National Forest between the years 1875 and 1896 and currently (2016), despite long fire rotations reported for high-elevation forests in the region. Over a century has occurred with limited fire within the Routt National Forest, according to historical accounts of fire cessation with the establishment of forest reserves. Factors that shift the balance from herbaceous plants to trees may encompass disrupted understory regimes through fire exclusion, large native herbivore extirpation, and overgrazing by domestic livestock combined with novel overstory regimes by the removal of trees, which has also provided some control of tree regeneration. Newly afforested areas may have become particularly vulnerable to decline through drought, climate change, and associated disturbances. Forestation in the Routt National Forest, Colorado, matches global patterns and processes after European settlement.

Author Contributions: B.B.H. performed analysis, visualization, and writing. J.M.S. performed investigation, data curation, and project administration. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Data available at https://glorecords.blm.gov/.

Acknowledgments: This research was supported by the USDA Forest Service, Rocky Mountain Research Station, and the FIA winter work program. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy.

Conflicts of Interest: The authors declare no conflicts of interest.

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