

# Forest closure and encroachment at the grassland interface: a century-scale analysis using oblique repeat photography

CHRISTOPHER A. STOCKDALE <sup>1,3,†</sup>, S. ELLEN MACDONALD,<sup>1</sup> AND ERIC HIGGS<sup>2</sup>

<sup>1</sup>Department of Renewable Resources, Faculty of Agricultural, Life and Environmental Sciences, University of Alberta, Edmonton, Alberta, Canada

<sup>2</sup>School of Environmental Studies, University of Victoria, Victoria, British Columbia, Canada

**Citation:** Stockdale, C. A., S. E. Macdonald, and E. Higgs. 2019. Forest closure and encroachment at the grassland interface: a century-scale analysis using oblique repeat photography. *Ecosphere* 10(6):e02774. 10.1002/ecs2.2774

**Abstract.** We used repeat oblique photography to quantify and determine the drivers of vegetation change, particularly forest closure and encroachment, in the Rocky Mountains of southern Alberta, Canada, from the beginning of the twentieth century to the present. We classified the landscape into seven distinct vegetation types (closed-canopy conifer forest, broadleaf deciduous forest, mixedwood forest, open-canopy woodlands, shrublands, grasslands and meadows, non-vegetated) and assessed vegetation change between the two time periods. We found that closed-canopy coniferous forest, broadleaf deciduous forest, and mixedwood forest increased on an area basis by 35%, 45%, and 80%, respectively, over this time period; concomitantly, grasslands and open-canopy woodlands declined by 25% and 39%, respectively. Overall, 28% of the landscape was in a more advanced successional state in 2008 as compared to the early twentieth century. The Montane and Subalpine Natural Subregions (NSR) experienced the most change (42% and 26%, respectively, in a more advanced successional state). The loss of open-canopy woodlands was observed across the entire landscape, while grassland and meadow losses were most acute in the Subalpine and Alpine NSRs. The probability of vegetation change to a more advanced successional condition was greater at higher elevations and in areas receiving lower amounts of solar insolation. The changes observed are consistent with what we would expect to see due to lengthening of fire return intervals. Understanding the magnitude of change in vegetation types and the drivers of this change is important for the development of effective contemporary ecosystem management and restoration practices.

**Key words:** change detection; ecosystem change; forest encroachment; historical ecology; repeat photography; vegetation change.

**Received** 21 September 2018; revised 14 April 2019; accepted 18 April 2019; final version received 14 May 2019. Corresponding Editor: Robert A. Washington-Allen.

**Copyright:** © 2019 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

<sup>3</sup>Present address: Northern Forestry Centre, Natural Resources Canada, Canadian Forest Service, 5320 122 St NW, Edmonton, Alberta T6H 3S5 Canada.

† **E-mail:** Chris.stockdale@canada.ca

## INTRODUCTION

Since the arrival of European settlers in the interior west of North America in the late nineteenth and early twentieth centuries, following earlier stages of exploration and fur trade in the earlier nineteenth century, fire regimes and vegetation composition changed considerably (Arno

1980, Barrett 1996, Bradley and Wallace 1996, Quigley and Arbelbide 1997, Heyerdahl et al. 2001, Hessburg and Agee 2003, Wright and Agee 2004, Van Wagner et al. 2006, Romme et al. 2009). Numerous studies show lengthening fire return intervals since the turn of the twentieth century (Hawkes 1979, Tande 1979, Arno 1980, Barrett 1996, Rogeau 1999, 2016, Heyerdahl et al.

2008). This was accompanied by substantial increases in closed-canopy forests, and a concomitant decline in grasslands and open-canopy woodlands, in the Rocky Mountains of the northern United States and Canada (Strong 1977, Gruell 1983, Campbell et al. 1994, Brown et al. 1999, Hessburg et al. 2000, 2005, Fulé et al. 2002, Rhemtulla et al. 2002, Higgs et al. 2009). While previous studies have documented these changes, they have not been able to provide a quantitative, area-based estimate, nor have they explored in detail the causal factors.

Understanding ecological history provides land managers with tools to manage present-day problems and is an essential component of ecological restoration (Quigley and Arbelbide 1997, Higgs et al. 2014, Beller et al. 2017). For example, regardless of the exact amount of forest encroachment that has occurred to date, there is growing evidence that these lower-diversity, closed-canopy, contiguous conifer (CF) forests are at elevated risk to loss by fire (Hessburg et al. 2000, Fulé et al. 2004, Moore et al. 2004, Prichard et al. 2017) and forest diseases and insects, such as the mountain pine beetle (Hughes et al. 2006, Dordel et al. 2008). While there is no single correct temporal reference point from which to evaluate change, the pre-European settlement period is widely used throughout North America for ecological restoration targets in the management of forests (Barrett et al. 2010), rangelands (Fuhlendorf and Engle 2001), and protected areas (White et al. 2003a, Higgs et al. 2014, Parks et al. 2014). There is recent concern about the emergence of novel ecosystems (ecosystems without historical analogue) as a result of directional environmental (e.g., climate, nitrogen deposition) and ecological (e.g., invasive species, disturbance regime) change, and shifts in land use conversation and occupancy. Well-resolved historical information provides reference targets for restoration but also guidance about how to manage adaptively to rapidly shifting ecosystems and landscapes (Hobbs et al. 2014).

Disturbance regimes and historical vegetation change are studied using a variety of techniques including (1) dendroecology (Barrett and Arno 1988) and stand reconstructions (Ehle and Baker 2003), (2) paleoecology (MacDonald et al. 1991, Carcaillet et al. 2001), (3) examination of historical records from fire occurrence databases

(Bergeron et al. 2001), maps (Johnson and Fryer 1987), and aerial imagery (Fichera 2012), (4) modeled using inputs derived from these sources of information (Collins et al. 2009, Wimberly and Kennedy 2008, Prichard et al. 2018), and (5) through oral histories (Lykke 2000). One largely untapped data source to examine landscape vegetation change is historical repeat photographs (images taken from the same place at two or more points in time). Historical repeat photography studies have shown forest invasion of grasslands across a wide geographic area of western North America from the late 1880s and early 1900s to the present day (Hastings and Turner 1965, Arno and Gruell 1983, Gruell 1983, Webb 1996). The primary limitation of these studies is that the changes were not spatially quantified. Newly developed techniques in oblique angle image analysis now enable rapid and accurate assessment of a large number of historical repeat photographs, facilitating spatial quantification of landscape-level changes (Stockdale et al. 2015, Fortin et al. 2018).

The Mountain Legacy Project ([mountainlegacy.ca](http://mountainlegacy.ca); MacLaren 2005, Trant et al. 2015) is a repeat photography project larger than any other similar project in the world with more than 120,000 historical images taken in the mountainous regions of western Canadian by numerous topographic map surveyors in the late nineteenth and early twentieth centuries. The collections are especially distinctive because survey photography ensures systematic coverage, triangulation of imagery and survey measurement, and high-quality resolution. To date, more than 7000 of these images have been repeated (in the southern Rockies from 1998 to present day) from the exact original locations (paired images). While some researchers have used these images to examine ecological change in focused locations (Rhemtulla et al. 2002, Watt-Gremm 2007, Kubian 2013, Fortin et al. 2018), their real potential to evaluate large spatial scale ecological change throughout the Alberta Rocky Mountain region has remained largely untapped.

The southern Alberta Rocky Mountain region in the centuries prior to the European settlement period can be examined from the perspective of human history to gain an understanding of how anthropogenic influences may have changed the landscape itself. The study region is home to the

Blackfoot Confederacy comprising three contemporary First Nations: the Siksika, Kainai, and Piikani. The Blackfoot First Nations hunted bison in numerous ways, including the use of prescribed fire and buffalo jumps, which were numerous throughout the region (Brink 2008). By the mid-1700s, with the introduction of diseases, horses, and guns, their way of life and methods of hunting began to fundamentally change (Brink 2008). The first European explorers (David Thompson, Peter Fidler, and others) came through the region in the late 1700s and early 1800s, which led to a period of active trade between the Blackfoot and Europeans, and ultimately the signing of treaties with the Canadian government in the 1870s; this effectively removed the free-moving connections the Blackfoot people had with traditional lands and moved them onto reservations (Brink 2008). This was followed by extirpation of the bison by 1880, the building of the railroad by 1897, and the founding of numerous European settlements in the region (Brink 2008). This period of change coincides with observed changes in fire frequency throughout the region, which were presumably the result of both increased suppression efforts by settlers and reduced burning by First Nations peoples. The Mountain Legacy Project images provide a clear snapshot of what the landscape looked like toward the end of this period of tumultuous change and can offer considerable insight into what it looked like prior to European settlement.

In this study, we use historical photographs to quantify the changes in vegetation composition since European settlement (late 1800s and early 1900s) in the southern Alberta Rocky Mountains and foothills and to examine which factors help explain variation in patterns of change across the landscape. We addressed three hypotheses: (1) vegetation across the landscape in 2008 is, overall, further along in succession than it was at the time of European settlement; (2) that there has been a loss of grasslands and open-canopy woodlands due to forest encroachment; and (3) the extent of these changes varies with: Natural Subregions (NSRs); topographic position (elevation, slope, and aspect); disturbance history (time since fire or timber harvest); and anthropogenic disturbance (AD; e.g., agriculture, settlements, roads, powerlines, railways, pipelines, and other rights-of-way).

## METHODS

### *Study area*

We used the Bridgland 1913–1914 phototopographic survey (Trant et al. 2015) to delimit the study area in the southern Rocky Mountains of Alberta (Fig. 1). These photographs were taken from 236 unique photographic locations (stations) and covered the area of the Rocky Mountains from the Alberta–British Columbia border to the Porcupine Hills and from the US–Canada border to Sentinel Pass (142 km to the north). In this region, the elevation range is from 1114 m to 3094 m above sea level; the area is dominated by mountainous terrain in the west, foothills to the east, and open grassland in the southeast and includes five different NSRs (Table 1; Natural Regions Committee 2006).

*Image selection.*—Paired repeat photographs of the Bridgland survey (MacLaren 2005) were used to assess landscape vegetation change across the study area (Fig. 2). The Government of Alberta supplied us with a high-resolution (1 m) Digital Elevation Model (DEM) that covered the majority of the southern Rocky Mountains and foothills region of Alberta. Using a GIS, we overlaid a 5-km grid across the area covered by the DEM and randomly chose two images taken within each cell, resulting in a total of 137 image pairs to be georeferenced and classified (not all cells had two images available). After georeferencing these images, we computed their viewsheds and found that numerous photographs shared large portions of their viewsheds with other photographs; we, therefore, discarded some images and randomly selected new ones iteratively until we had maximized the total landscape coverage at 57.4% of the total study area (Table 1). See Stockdale (2017) and Appendix S1: Section 1 for a full description of image selection methods. With oblique imagery, the parts of the landscape behind topographic barriers are not visible; by using images taken from numerous locations, we determined that the area visible in the 137 image pairs was representative of the greater landscape with respect to the distribution of NSR and solar insolation (Appendix S1: Fig. S1).

### *Image georeferencing, vegetation classification, and disturbances*

We used the methods developed by Stockdale et al. (2015) using the WSL Monoplotting Tool

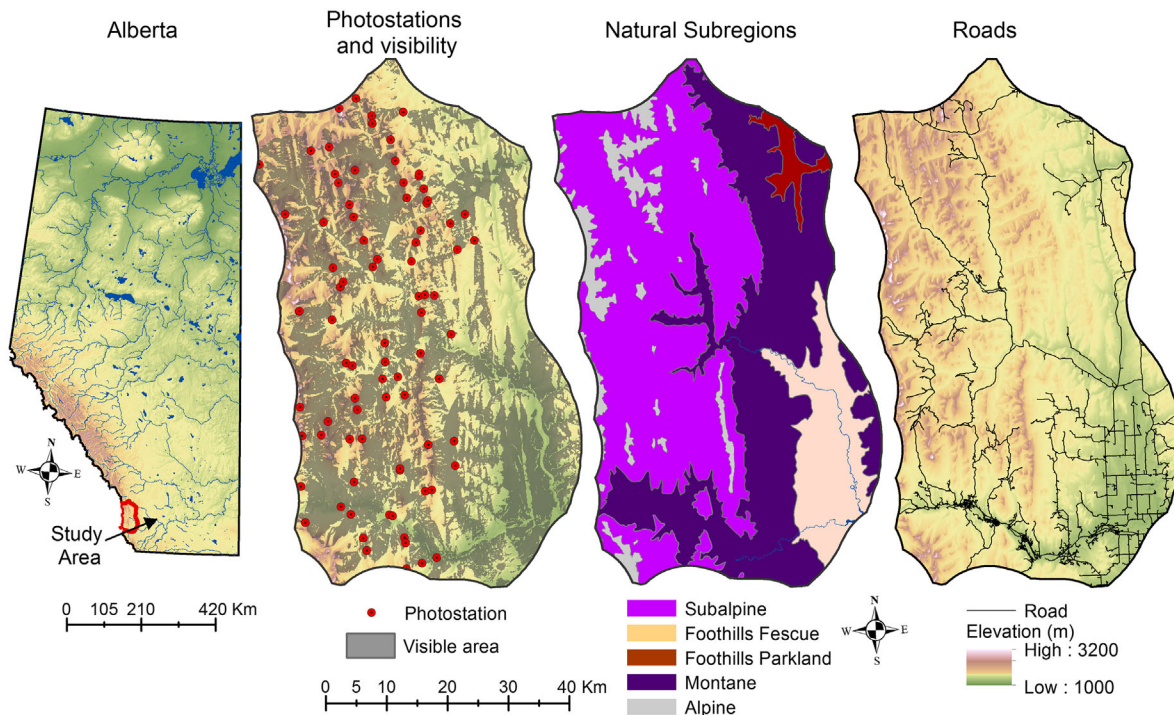


Fig. 1. The map panels (left to right) show the location of the study area in the southwestern corner of the province of Alberta, the locations of photostations from the Bridgland 1913–1914 survey used in the study along with the total visible area of the landscape from 137 paired photographs, the Natural Subregions of the area, and elevation and the locations of the roads in the study area.

Table 1. Distribution (area and %) of the different Natural Subregions within the entire study area and within the portion of the study area that was visible in the selected images; also given is the percentage of each subregion that was visible.

Natural subregion†	Study Area (ha)	% of Total study area	Visible area (ha)	% of Total visible area	Visible as % of study area
Alpine	14,468	4.5	9058	5.0	62.6
Subalpine	144,611	45.4	86,092	47.2	59.5
Montane	117,091	36.8	59,636	32.7	50.9
Foothills Fescue	35,990	11.3	25,282	13.8	70.2
Foothills Parkland	6140	1.9	2515	1.4	40.1
TOTAL	318,300	100	182,583	100	57.4

† Natural Regions Committee (2006).

(Bozzini et al. 2012) to georeference and classify vegetation in grid cells in each repeat photograph pair. Each image was georeferenced, and we then computed its viewshed. Viewsheds were restricted to the distance from the camera station at which we could confidently discern vegetation categories; this distance was variable, but the maximum distance generally ranged

from 5 to 10 km but was sometimes more depending on the clarity in a particular photograph. In the case of images that looked out over the grasslands to the east, two images were assessed to a distance of ~25 km. We then intersected a 1-ha spatially referenced grid with this restricted viewshed to yield an image visible grid. We transformed this image visible grid



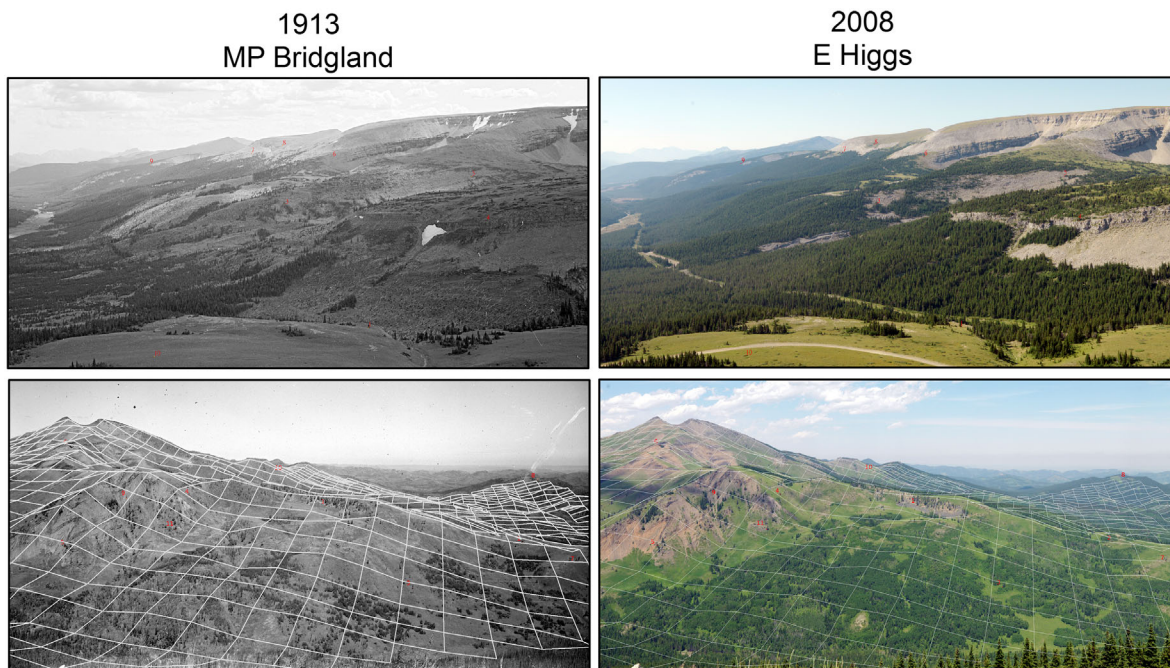


Fig. 2. Mountain Legacy Project paired photographs from the 1913–1914 Bridgland Survey repeated in 2008 by the Mountain Legacy Project. The second row shows an image pair with a georeferenced 1-ha grid overlaid. This overlay grid was used to classify vegetation within each cell to measure change between the two time periods. The images pairs were taken from Station 53, Sentinel Pass West No. 1, and Station 45, Riley Creek No. 3 for the first and second image pairs (respectively). See [explore.mountainlegacy.ca](http://explore.mountainlegacy.ca).

from the orthogonal view to the oblique view and overlaid it on the image to be classified (Fig. 2). See Appendix S1: Section 2 and Stockdale (2017) for further details on the georeferencing and grid overlay procedures.

We classified the vegetation in each visible grid cell as one of seven vegetation types: non-vegetated (NV), meadow and grassland (MG), shrubland (SH), open-canopy woodland (WD), broadleaf deciduous (BD), mixedwood (MX), or CF. See Appendix S1: Section 3, Table S1, and Figs. S2–S4 for a full description and examples of the vegetation classes and how they were discerned in the photographs. These broad classes were used because it was very difficult to discern species at a distance, and in the original (black and white) photographs, species were virtually impossible to discern. Nevertheless, we know that the dominant tree species in each vegetation class varied among NSR as follows. The dominant tree species in the CF vegetation type in the Subalpine NSR were lodgepole pine (*Pinus*

*contorta*), subalpine fir (*Abies lasiocarpa*), or Engelmann spruce (*Picea engelmannii*), and in the Montane NSR primarily lodgepole pine or Douglas-fir (*Pseudotsuga menziesii*). In wetter parts of the Subalpine and Montane NSRs, there were pockets of black spruce (*Picea mariana*). Trees in the broadleaf (BD) vegetation type in the Foothills Fescue, Montane, and Subalpine NSRs were trembling aspen (*Populus tremuloides*), or on wetter and riparian sites balsam poplar (*Populus balsamifera*). The dominant trees in the MX forest vegetation type in all NSRs included aspen and CF (lodgepole pine, Douglas-fir, or Engelmann spruce). Trees in the woodland (WD) vegetation type in the Alpine and Subalpine NSRs were lodgepole pine, subalpine fir, limber pine (*Pinus flexilis*), and occasionally whitebark pine (*Pinus albicaulis*) or Engelmann spruce. In the Montane NSR, the dominant trees in the woodland class were lodgepole pine, subalpine fir, Douglas-fir, Engelmann spruce, trembling aspen, or balsam poplar. In the grasslands, isolated stands of trees

included lodgepole pine, Douglas-fir, aspen, or balsam poplar.

The original and repeat photographs for each photograph pair were examined together by overlaying them in GIMP in order to better distinguish vegetation categories in the repeat and original images. Where possible, difficult-to-classify areas of the landscape were examined from other photographs in the Bridgland survey that showed the same location from a different angle and distance. In cases where it was not clear (due to photographic quality, extreme shadow, or other uncertainty) what vegetation category a particular cell should be classified as in either the original or repeat photograph, the grid cells were removed from the analysis and not considered any further. After we classified each image pair, the visible grid cells were added to a cumulative total area assessed layer. For every subsequent image analyzed, we subtracted the total area assessed from its image visible grid so that each visible grid cell on the landscape was only assessed in a single image. In total, the 137 image pairs yielded a visible area of 182,583 ha. From this image analysis, we developed two vegetation layers (one each for 1913 and 2008), hereafter referred to as Veg1913 and Veg2008.

In both the original and repeat photographs, recently burned forests were evident. Large fires had burned through the study area in 1910 and in 2003 (very southern edge of our study area). Had we used 1913 as our baseline, we would have been comparing the present-day landscape to a point in time immediately after one of the most extensive fire years on record and this could have exaggerated the amount of long-term change that had occurred on the landscape (we ended up labeling 8% of the landscape [see *Results* below] as non-forest in 1913 due to the 1910 wildfires). In order to better represent the historical landscape prior to European settlement of the region, we rolled back vegetation categories from 1913 to the year before the fire (1909). This led to a comparison that reflects a more conservative estimate of change, but one that more accurately reflects the pre-European settlement landscape condition. This rollback created a third time layer of 1909 (layer Veg1909), which was achieved by examining the grid cells showing recent fire in the Veg1913 layer to determine what they most likely had been in 1909.

Grid cells in which evidence of fire was visible were classified as disturbed fire (DF), and then, the 1909 vegetation category was determined by the vegetation structure in these cells. Disturbed fire grid cells with very few live or dead trees were classified as grassland (MG), those with a low of density snags were classified as WD, if there were dense coniferous snags they were classified as CF, mixed broadleaf and CF snags as MX, and broadleaf snags as BD. This method failed to detect any fires that burned (1) at low severity causing no visible overstory mortality; (2) at such high severity that all dead wood was burned away completely; (3) through grasslands leaving no evidence. All subsequent analyses compare the Veg1909 to the Veg2008 layers.

To track other disturbances, grid cells with evidence of anthropogenic disturbance (AD) from development such as agricultural cropland, roads, buildings, settlements, powerlines, and rail lines were classified as AD and the vegetation category was based on the dominant vegetation form or labeled as non-vegetated if the cell was fully developed (road, house, building, gravel). For the purposes of this analysis, agricultural crops were classified as grassland (MG). We also classified areas that were visibly fenced (indicative of private ownership) as agricultural (AG), but this was more difficult to assess in the historic black and white images (when fencing was also less common) than in the repeat color images; the difficulty in discriminating agricultural lands from native grasslands in the original images is the primary reason we did not track agricultural land conversion in this study.

Lacking the ability to ground truth the historical photographs, we assessed the reliability of our classification by conducting three tests in which we compared (1) oblique photograph versus ortho-photograph classifications of the same areas, (2), agreement between our vegetation classification calls in color oblique images compared to two independent observers, and (3) level of agreement between the primary observer and two independent observers as to whether vegetation had changed from 1912 to 2008 in the MLP image pairs. Details of these comparisons are in Appendix S1: Section 4, Tables S2–S4), with the first two comparisons presented as confusion matrices. Based on these assessments, we are confident in our classification.

### Vegetation change and transitions

We created a transition matrix and tallied all unique ( $7 \times 7 = 49$ ) vegetation transitions between 1909 and 2008. We assumed the successional pathway was from non-vegetated to meadow/grassland to shrub to open canopied woodland to forest (broadleaf then mixed then coniferous, i.e., NV-MG-SH-WD-BD-MX-CF; Archibald et al. 1996). We were particularly interested in the fate of historical grassland and woodland areas of the landscape for these cells (Veg1909 = MG or WD).

### Other data layers

We obtained spatial data on linear features (roads, cut lines, trails, railways, pipelines), timber harvest records, and fire polygons from 1931 to 2008 from the Government of Alberta. We excluded all fires smaller than 1 ha from the fire history records, and these were combined with fires observed in the Veg1913 layer to create a 1909–2008 fire history. We buffered linear features (highways and railways by 300 m on both sides, all other linear features by 100 m both sides) to account for edge effects and merged these into the observed AD cells to create a single coverage of AD (Fig. 3).

To account for the effect of slope and aspect, we used solar insolation as it combines the influence of both variables in a single continuous predictor. See Appendix S1: Section 5 for a description of how watersheds were delineated and insolation was calculated.

We found evidence of spatial autocorrelation in the response variable successional change (see below; Moran's  $I$ -statistic = 0.4203,  $z$ -score = 784.57,  $P < 0.000001$ ). This indicated clustering in successional change, with a distance threshold of 1118 m. We also found that there was significant spatial autocorrelation in both the MG and WD change response variables (more below; Moran's  $I$ -statistics = 0.596 [MG], 0.490 [WD],  $z$ -scores = 734.71 [MG], 123.9 [WD],  $P$ -values for both  $< 0.000001$ ). These results indicated clustering in the response variables with distance thresholds of 2561.5 m (MG) and 2524.1 m (WD). To control for this spatial autocorrelation in the data in the subsequent statistical analyses, watersheds (see Fig. 3) were constructed to serve as a random block effect.

### Data analyses

To examine overall patterns of vegetation change we created a response variable called successional change between the two periods based on the vegetation class (same [0], forward [+1], or reverse [−1]; see successional pathway sequence above, and Table 2). We used a chi-square analysis to test the hypothesis that there was a difference in the distribution of successional change values by NSR. We tested whether successional change was spatially randomly distributed on the landscape by calculating Moran's  $I$ -statistic using the Spatial Autocorrelation (Moran's  $I$ ) tool in ArcGIS 10.4. We used ordinal logistic regression (R Package Ordinal, procedure CLMM) to examine the relationship between successional change (ordinal values of −1, 0, 1 as indicated above) and two continuous predictor variables (mean solar radiation, elevation) and three categorical predictor variables (time since fire [TSF], time since harvest [TSH], AD). All visible grid cells were used in this analysis ( $n = 182,583$ ) and were nested within watersheds (included as a random block effect) to account for spatial autocorrelation (details in Appendix S1: Section 6). We computed the Spearman's rho statistic to determine whether predictor variables were correlated with one another. We ran models including all permutations of predictor variables and an ecological null model that included only the watershed random factor. The best model was chosen by the lowest Akaike Information Criterion (AIC) value.

To determine whether successional change (forward, no change, reverse) in former grassland or woodland portions of the landscape varied among NSR, we used chi-square tests for MG and WD separately. To determine whether grassland loss was occurring primarily adjacent to historical forest edge, we converted the vegetation transition raster layer into polygons to group all like transitions: grassland lost; grassland gained; grassland retained. We measured the length of all boundaries between grassland lost and non-grassland vegetation types. We used the same procedure to determine whether open-canopy woodlands were being lost primarily adjacent to historical forest edges.

To examine factors explaining variation in patterns of change from grassland or woodlands, we used ordinal logistic regression with the



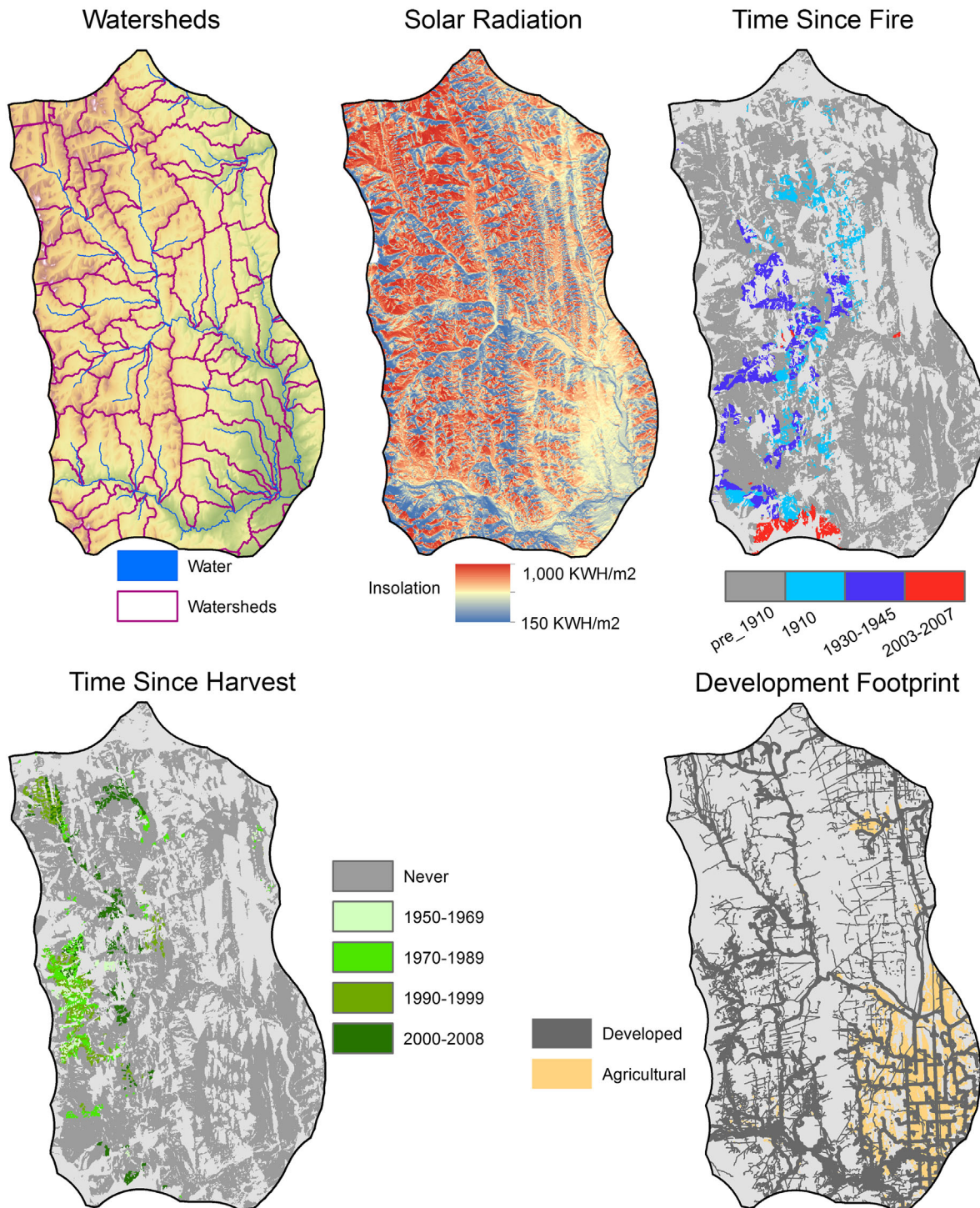


Fig. 3. Spatial data layers accounting for watersheds, solar insolation, time since fire (TSF), time since harvest (TSH), and the development footprint of the landscape (AD, which combines agricultural and anthropogenic development). The palest gray background color in the TSF and TSH maps indicates areas that were not visible in the images we selected for analysis.



Table 2. Vegetation transitions between 1909 and 2008 as a percentage of the visible area in each vegetation class in 1909.

Vegetation 2008	Vegetation 1909						
	NV (5.6%)	MG (42.2%)	SH (3.6%)	WD (6.9%)	BD (3.9%)	MX (2.9%)	CF (35%)
Reverse	n/a	0.016	0.165	0.130	0.237	0.247	0.141
NV (5.5%)	<b>0.795</b>	0.016	0.009	0.018	0.011	0.013	0.002
MG (31.7%)	0.083	<b>0.611</b>	0.156	0.111	0.212	0.082	0.088
SH (0.5%)	0.004	0.007	<b>0.034</b>	0.001	0.006	0.003	0.000
WD (4.2%)	0.054	0.051	0.040	<b>0.102</b>	0.008	0.028	0.024
BD (5.6%)	0.300	0.051	0.311	0.033	<b>0.412</b>	0.121	0.005
MX (5.2%)	0.005	0.041	0.192	0.077	0.198	<b>0.246</b>	0.021
CF (47.3%)	0.057	0.222	0.259	0.659	0.154	0.507	<b>0.859</b>
Forward	0.205	0.372	0.802	0.769	0.352	0.507	n/a

Notes: Columns add to 1 to account for all transitions from that class. The values in parentheses with each vegetation class on the top row and right column are the percent of the visible landscape that was in that vegetation category in 1909 and 2008, respectively. To determine the proportion of the landscape going through any transition, multiply the value in the cells by the value in parentheses. Values in boldface indicate no change, cells above the diagonal changed to an earlier successional state (reverse succession in Table 3), and cells below changed to a more advanced successional state (forward succession in Table 3) in 2008 relative to 1909. NV, non-vegetated; MG, meadow/grass; SH, shrub; WD, woodland; BD, broadleaf deciduous; MX, mixedwood; CF, conifer.

response variable of successional change as indicated above (separate analyses for grasslands and woodlands) with the same predictor variables described in the previous paragraph (without TSH, as there had been no harvesting in the former grasslands or open woodlands) and model selection criteria. The response variable was the degree of vegetation change, coded to indicate reverse succession (−1), no change (0), and forward change (values of 1–3 to indicate the degree of change, see Appendix S1: Table S5). We tested for spatial autocorrelation in the response variable using the Spatial Autocorrelation (Moran's *I*) tool in ArcGIS 10.4.

## RESULTS

### Vegetation succession

Grasslands occupied 42.2% of the landscape in 1909, coniferous forest occupied 35%, while all other categories combined occupied 22.8% of the landscape (Fig. 4, Table 2). In 2008, 47.3% was coniferous forest, grasslands occupied 31.7%, and the remaining categories combined occupied 21% of the landscape. The most stable vegetation categories were coniferous forest (85.9% remained the same, which represents 30% of the landscape) and meadow/grassland (61.1% remained the same, which represents ~26% of the landscape; Table 2). The closed-canopy forest portion of the landscape increased from 41.8% to 58.1%

of the area over this time period (Table 2). 13% of area that was grasslands and 5% of the area that had been open-canopy woodland had become closed-canopy forest by 2008 for a net 18% increase in forest cover.

Overall, 63.4% of locations had no change in vegetation categories, 27.8% of the landscape was in a more advanced successional state, and 8.7% was in an earlier successional state (Table 3). There was a significant difference among NSRs in the proportional area showing no, reverse, or forward successional change ( $P < 0.0001$ , Pearson's chi-squared = 16982, degrees of freedom = 8): The Montane NSR had the most area (41.6%) showing forward succession, followed in diminishing order by Foothills Parkland (29.4%), Subalpine (26%), Alpine (25.7%), and Foothills Fescue NSRs (2.3%; Table 3). The Foothills Parkland NSR showed the most reverse succession (14%), followed by the Montane NSR (10.2%). There were significant differences among the NSRs in terms of the probability of reverse, forward, or no succession for areas that were meadow/grassland or woodland in 1909 (Table 3,  $P < 0.0001$ ; Pearson's chi-squared = 27910 [MG] and 3109.7 [WD], degrees of freedom = 8 for both).

### Forest encroachment

The greatest transition in vegetation types on the landscape was from meadow/grassland to

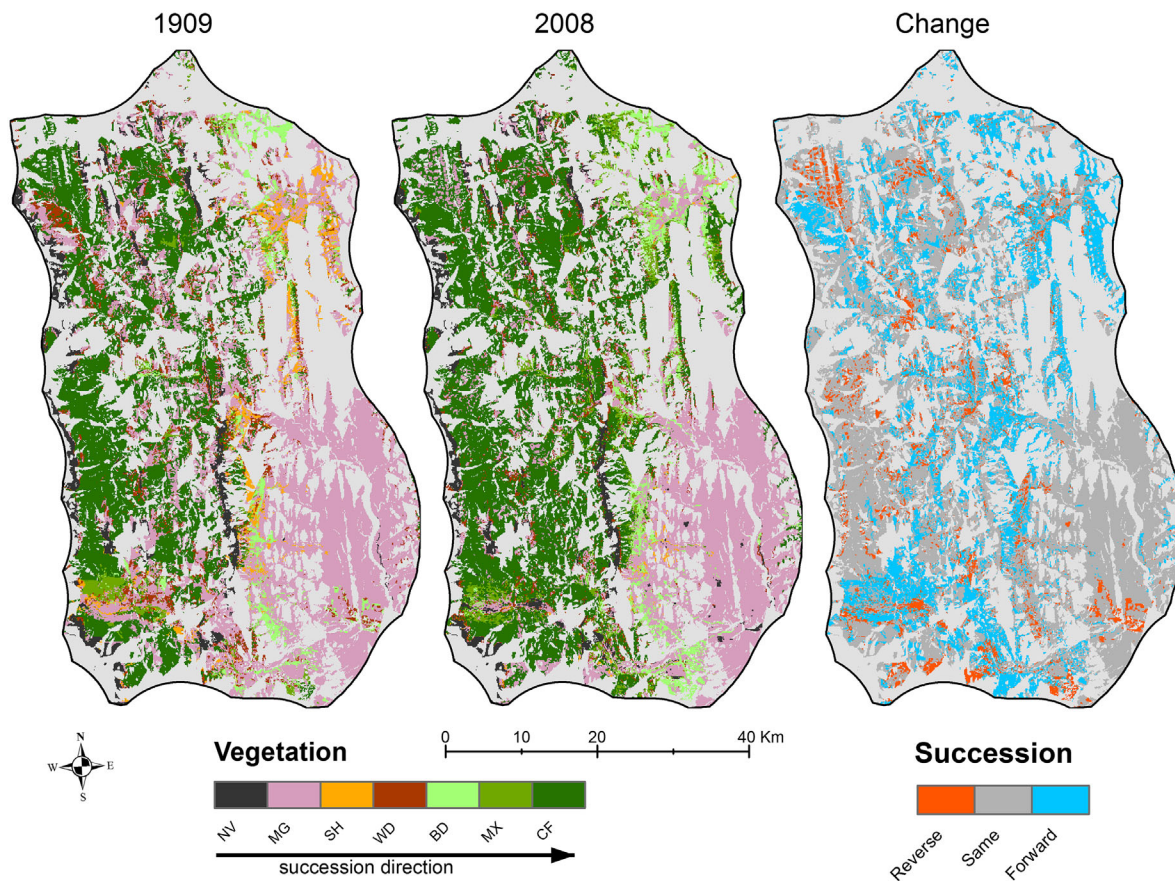


Fig. 4. Vegetation across the landscape in 1909 and 2008 as measured from 137 historical repeat photography pairs. The vegetation categories are non-vegetated (NV), meadows and grassland (MG), shrubland (SH), open-canopy woodland (WD), broadleaf deciduous (BD), mixedwood (MX), and coniferous (CF). The successional sequence of these vegetation types is indicated, as is the overall direction of successional change on the landscape. Reverse indicates that in 2008 the vegetation at a given location is at an earlier successional state than it was in 1909, same indicates it has not changed, and forward indicates that in 2008 the vegetation was in a more advanced successional state than it was in 1909. The pale gray background color in each map indicates areas that were not visible in the images we selected for analysis.

coniferous forests (9.4%), with substantial transition from grassland to the other closed forest types (MX = 1.7%, or BD = 2.2%). Combined, 18.5% of the visible landscape changed from grassland/meadow (MG) and open-canopy woodland (WD) in 1909 to closed-canopy forest (BD, MX, CF). Of the parts of the landscape that were grassland or woodland that converted to forest between 1909 and 2008, 67% and 45% of the edge of new forests occurring in historic grasslands and open-canopy woodlands (respectively) shared this edge boundary

with historic forests (these figures are 94% and 85% for grassland and woodland, respectively, when considering the area of new forests occurring next to historic forests; Table 4, Fig. 5). To calculate the proportion of the landscape that changed from one category to another, use Table 2, and multiply the proportion of landscape covered by a given vegetation type in 1909 (value in parentheses on the top row) by the values in the table for the specific transition of interest (e.g., MG transition to CF:  $42.2\% \times 0.222 = 9.4\%$ ).

Table 3. Vegetation change, as percentage of visible area, classified as direction of succession for the whole landscape and by Natural Subregion.

Vegetation succession direction	Total landscape	Natural Subregion														
		Alpine (%)			Subalpine (%)			Montane (%)			Foothills Parkland (%)			Foothills Fescue (%)		
		All	MG	WD	All	MG	WD	All	MG	WD	All	MG	WD	All	MG	WD
Reverse	8.7	4.2	9.8	10.3	9.3	1.7	8.1	10.2	1.8	12.1	14	0	20	4.4	0.1	97.8
Same	63.4	70.1	35.7	13.8	64.7	19.6	11.3	48.3	58.2	8.9	56.6	73.4	0	93.3	97	0.7
Forward	27.8	25.7	54.5	75.9	26.0	78.7	80.5	41.6	40	79	29.4	26.6	80	2.3	2.9	1.5

Notes: Results are given for overall successional change of vegetation and for areas that were meadow/grasslands (MG) or open-canopy woodlands (WD) in 1909 by Natural Subregion. These numbers relate to Table 2, where the totals above and below the diagonal no change line have been weighted by their total landscape cover proportions. See also Fig. 4.

Table 4. Area of grasslands or open-canopy woodlands lost between 1909 and 2008; given is total area lost (changed to later successional state), the total length of edge of that area for which the neighboring area was visible, the percentage of that edge length and of the area that bordered forests in 1909.

Historic vegetation lost	Area lost (ha)	Edge with neighbor		Percentage touching forest	
		Length (km)	Percentage	Edge	Area
Grassland	29,936	3930	73.2	67.2	94.2
Woodland	11,311	1971	75.7	45.6	84.5

Note: For the grassland historic vegetation, "forest" includes open-canopy woodlands and all forest types; for the woodland, this includes all forest types.

#### Influences of topography and disturbance history

Of the small percentage (15,492 ha, or 8.7%) of the landscape in an earlier successional state in 2008; nearly all of this (13,453 ha, or 87%) had undergone harvesting (4170 ha, or 26.2%), been burned (3756 ha, or 23.5%), or has some other AD (5527 ha, or 34.7%) between the two time periods.

The best model (Table 5) for overall vegetation successional change included solar radiation, elevation, TSH, TSF, and AD (see Appendix S1: Section 6 for a summary of all models). Solar insolation was negatively related to forward successional change (higher insolation = less change). Sites with a longer time since harvest or fire were more likely to have returned to or surpassed their pre-disturbance successional state. Elevation was positively related, and AD was negatively related to the probability of forward

succession. Spearman rank correlations revealed no strong correlations between the predictor variables (highest rho was  $-0.3184$  between AD and Elevation, all other rho  $< \pm 0.2$ ).

The best models of vegetation change for areas categorized as meadow or grassland (MG) and woodland (WD) in 1909 included solar radiation, elevation, and time since fire (Table 6a, b; see Appendix S1: Section 6 for a summary of all models). For areas that were MG or WD in 1909, solar insolation was negatively related to the probability of forward succession (Table 6a, b). For both vegetation types, areas with longer times-since-fire had higher probabilities of forward succession (Table 6). Elevation was positively related to the probability of forward succession for meadows/grasslands, but woodland areas at higher elevation had a decreased probability of forward succession. We found no strong correlations between predictor variables, with no rho values greater than  $\pm 0.25$ .

#### Vegetation classification accuracy

Our assessment of the vegetation classification accuracy (more details in Appendix S1: Section 4) showed that orthogonal versus oblique vegetation classification had 69.7% agreement; in the 30.3% with disagreement, 13% of the cells were classed as WD in the orthogonal view, but closed-canopy forest (CF, MX, or BD) in the oblique imagery. Some of the remaining 17% of disagreement likely stems from patch edge displacement, where the georeferencing methods produce small-scale horizontal displacement of grid cells (a grid cell in an oblique image might be located on a patch of trees, but once this is georeferenced, it might be placed in the adjacent



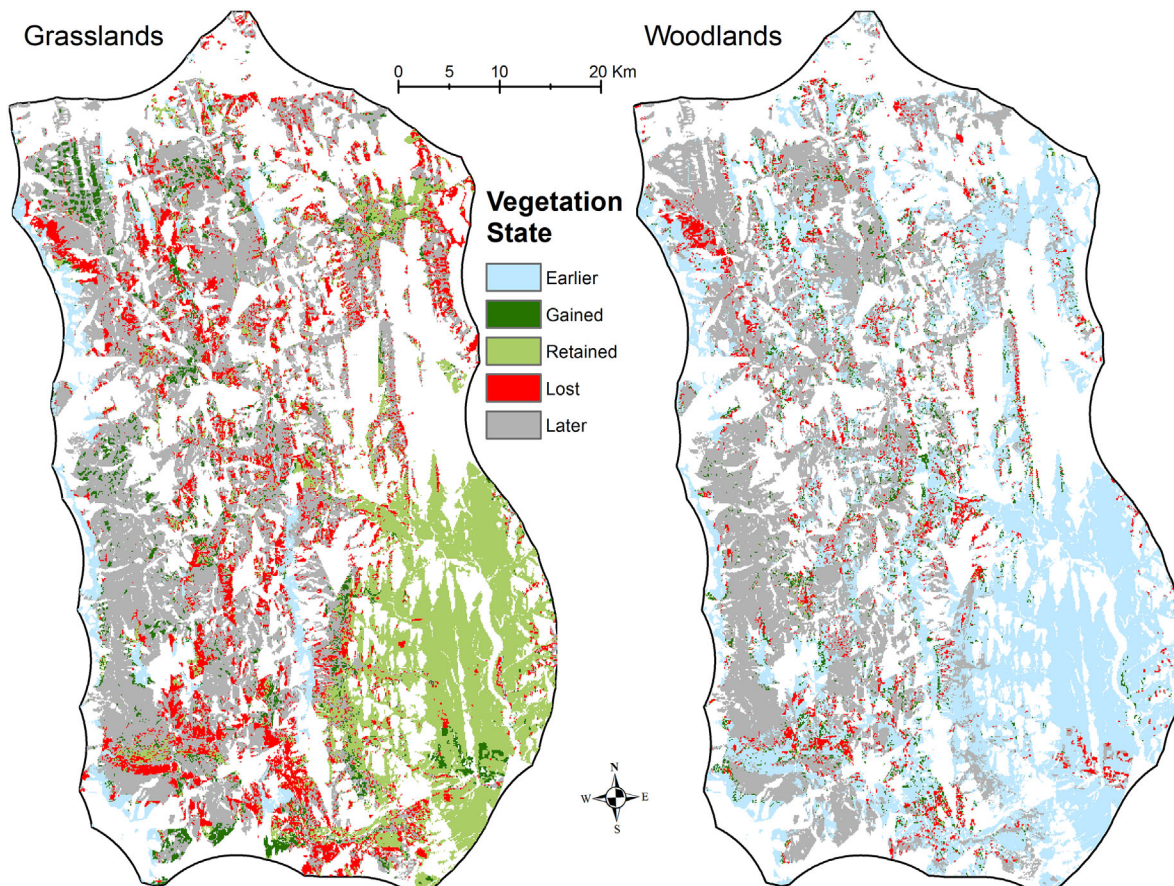


Fig. 5. Vegetation change for areas that were grassland or open-canopy woodland in 1909. The vegetation state refers to whether the targeted vegetation type (grasslands or woodland) was gained (not present in 1909, present in 2008), lost (present in 1909, not present in 2008), or retained (present in both 1909 and 2008) over the time period. These classifications only include vegetation that moved into or out of a meadow/grassland (first panel) or woodland (second panel) state. Earlier indicates areas where the vegetation was in an earlier successional state (i.e., for grasslands this only includes non-vegetated; for woodlands, this includes non-vegetated + grassland + shrubland). Later indicates areas where the vegetation was in a more advanced successional state (i.e., for grasslands map, this includes shrub + woodland + mixedwood + broadleaf deciduous + conifer (CF); for woodlands, this includes mixedwood + broadleaf deciduous + CF).

clearing on an ortho image; while the error in displacement might only be 100 m (for example), it can result in a different classification call, and be considered an error, when in fact the classification is correct, but the location is wrong). The agreement in orthogonal versus oblique classification in BD and MX classes was low (20% and 49.9%, respectively). In both of these classes, much (20% and 25.4%, respectively) of the disagreement was the result of under-classification of open-canopy forest. Half of what was

considered BD in the oblique images was classified as MX in the ortho images (short CFs may have been obscured at an oblique angle but visible from above). Thus, we may have overestimated BD, and underestimated MX. Most errors in oblique-classified MX were ortho-classified as CF, which suggests a higher CF content in stands classified as MX; they appear to have a higher amount of BD cover in oblique versus ortho-photographs. There was 80.5% agreement between the primary and independent accuracy-

Table 5. Outputs of the best ordinal logistic regression model for landscape vegetation change.

Variable	Estimate	Standard error
Z.solar	-0.036	0.005
TSH (1990s)	0.397	0.043
TSH (1970–1989)	1.707	0.047
TSH (1950–1969)	1.610	0.059
TSH (never)	2.489	0.032
TSF (1930–1945)	1.842	0.062
TSF (1910)	0.243	0.060
TSF (<1910)	2.150	0.058
AD	-0.069	0.011
Z.elev	0.209	0.009

*Notes:* The response variable was the succession with values of -1 for reverse, 0 for no change, and 1 for forward. The reference categories for TSH (time since harvest) and TSF (time since fire) are harvesting and fires, respectively, in the most recent time period. Z.solar and Z.elev indicate solar insolation and elevation transformed to z-scores. AD is the presence or absence of anthropogenic disturbance within a grid cell or buffer zone (see *Methods*). See also Figs. 3 and 4.

assessment observers. Most disagreement was the result of the thresholds for classifying WD or closed-canopy forest (CF, MX, or BD), or WD and MG. Independent observers agreed with 82.1% of the assessments of the primary observer with respect to whether vegetation cover had changed between the two time periods.

## DISCUSSION

In this study, we confirmed that vegetation in 2008 was further along in succession than at the time of European settlement, that significant forest encroachment has resulted in a loss of grasslands and open-canopy woodlands, and that variability in these trends was correlated with the influences of NSRs, topography, and natural and AD history. While the majority of the landscape in our study area remained in the same vegetation category in 2008 as it had been in 1909, we saw a substantial amount (18%) of the landscape converted to closed-canopy forest. Many areas that were grasslands in 1909 had changed to open-canopy woodland by 2008 and were thus on an apparent trajectory to closed-canopy forests. While a large portion (37%) of the original grasslands present in 1909 were in a more successional advanced vegetation type in 2008, this was partially offset by disturbances within other vegetation types that created new

Table 6. Outputs of the best ordinal logistic regression model for the magnitude of vegetation change for areas that were (a) meadow or grassland, or (b) open-canopy woodland in 1909.

Variable	Estimate	Standard error
(a) Meadow or grassland		
Z.solar	-0.545	0.010
TSF (1930–1945)	1.602	0.100
TSF (<1910)	1.582	0.093
Z.elev	1.074	0.017
(b) Open-canopy woodland		
Z.solar	-0.147	0.022
TSF (1930–1945)	3.654	0.294
TSF (<1910)	4.320	0.285
Z.elev	-0.146	0.037

*Notes:* The response variable was the magnitude of change variable which indicates the degree of succession occurring at a given location (Table A.5; Fig. 4). The reference category for TSF (time since fire) was fires that burned in the most recent time period (2003–2007). Z.solar and Z.elev indicate solar insolation and elevation transformed to z-scores. See also Figs. 3 and 5.

grasslands, resulting in a net loss in grassland area of only 25% between 1909 and 2008. Similarly, a large majority (nearly 80%) of the open-canopy woodlands from 1909 had succeeded to more advanced vegetation types in 2008, but this was partly offset by other vegetation types converting to open-canopy woodlands. Thus, there was a net loss of woodland area of only 39%.

As predicted, loss of meadows/grasslands and woodlands was largely due to forest encroachment, as evidenced by the fact that the majority of the area lost in these vegetation types was adjacent to existing higher-density forest. However, these patterns of increasing forest cover were not homogenous across the entire landscape. The Montane NSR, which is at a relatively lower elevation, had the greatest proportion of area undergoing successional advancement, while the Subalpine, Alpine, and Foothills Parkland NSRs had less, but still substantial forward change. The grassland losses in the Montane NSR were considerably lower than they were in the Subalpine NSR, perhaps due to less forest from which there could be encroachment. In the Alpine NSR, where forest encroachment into meadows/grasslands could only occur from lower elevation forests (with the higher elevation ecotone bordering on bare rock and talus slopes), we saw lower rates of forest encroachment. We

did not differentiate grasslands or meadows other than to define them as areas with no significant amount of trees or shrubs. In the Foothills Fescue NSR, the extensive anthropogenic footprint has converted much of the grasslands into agricultural land (grazing and ranching). In the absence of agricultural land conversion, we suspect there would have been more conversion of grassland to forest.

Our observations of forest encroachment concur with other studies. A study using pollen from sediment cores extracted from lakes throughout southern Alberta found areas that were aspen parkland proper in the 1970s had been groveland in the pre-European settlement (1800s) era, while groveland areas had previously been fescue grasslands (Strong 1977). Campbell et al. (1994) showed a biome-wide expansion of aspen into former grasslands dating to the 1880s and 1890s along the margin of what is now referred to as the aspen parkland across western Canada. Hessburg and Agee (2003) described widespread forest encroachment on grasslands throughout the inland northwestern United States (Montana, Idaho, Washington, and Oregon). However, our results contrast with those of Johnson and Fryer (1987), who found no evidence of landscape-scale vegetation changes between 1883 and 1972 just north of our study area. Johnson and Fryer (1987) examined a smaller landscape, focused exclusively on the Subalpine NSR using forestry survey records, and thus only examined historical sites with commercially valuable trees, thereby excluding open-canopy woodland or grasslands from their analysis.

Our findings do not tell us whether the composition of the CF forest itself changed or not over this time period because we could not reliably differentiate age or size classes of CF trees in the original black and white photographs. Furthermore, we did not differentiate ratios of broadleaf deciduous to coniferous trees in our mixedwood category, and the open-canopy woodland category varied from grasslands intermingled with single or clustered trees, to talus slopes with krummholz, to grassland with interspersed aspen copses. It seems likely, however, that much of the forest that remained as such over this time period was transitioning toward older age classes; shifts toward older age-class distributions in coniferous forests over this time period

have been shown throughout the Rocky Mountains (Gruell 1983, Johnson et al. 1994, Andison 1998, Rhemtulla et al. 2002, Hessburg et al. 2005).

Higher elevation areas experienced significant conversion of meadows and grasslands to forest, and this is consistent with other studies showing treeline advancement throughout the Rocky Mountains in the twentieth century (Luckman and Kavanagh 2000, Klasner and Fagre 2002, Shaw 2009, Elliott 2011, McCaffrey and Hopkinson 2017). We also saw much of the lowest elevation areas (agricultural zone) transitioned to earlier seral stages. We were therefore surprised to find that there was a negative influence of elevation on forward succession in our statistical model (i.e., higher elevation areas showed lower likelihood of forward succession). This may be explained by the observation that even though the lower elevation Montane and Subalpine NSR areas showed 80% conversion of the open-canopy woodlands to closed-canopy forest, there was a large area of the landscape occupied by agriculture and settlement where AD prevented forward succession. This occurred in the lowest elevation areas, which are largely in the Foothills Fescue NSR and some of the Montane NSR). We also observed significant conversion of open-canopy woodlands to closed-canopy forest in the Alpine NSR. However, many high-elevation open-canopy woodlands occurred on rocky outcrops, high-slope talus fields, and scattered krummholz stands and therefore were successional limited by available substrate. These may help explain the overall negative effect of elevation on forward vegetation succession in open-canopy woodlands. Furthermore, the observed negative effect of increasing solar radiation on the likelihood of forward succession could be owed to drier sites being more limited in their potential to develop forest cover.

The observed seral stage advancement of the landscape suggests a changed disturbance regime, and indeed, there is evidence that the annual area burned in these areas has declined dramatically since pre-1900. We found that time since disturbance was positively correlated with increasing likelihood of forward succession, and it appears as though the mean time since disturbance across the landscape has been increasing since European settlement. Rogeau (2016) found



historic (pre-1900) mean fire return intervals in the Montane and Subalpine NSRs of this landscape ranged between 35 and 150 yr. If we assume a ~100-yr fire cycle, we should see a 1% annual burn rate. However, we found that while wildfire burned roughly 8% of the study area in 1910 alone (with significant evidence of other recent fires that had recovered to vegetative cover in 1913), only 8.5% of our visible study area burned over the subsequent 95 yr (1913–2008). This equates to a post-1913 annual burn rate of 0.075%, which would produce a fire cycle (inverse of the burn rate) of 1333 yr.

Numerous studies describe the effects of twentieth-century fire exclusion on vegetation change (Baker 1992, Arno et al. 2000, Gallant et al. 2003, Hessburg and Agee 2003, Daniels et al. 2011, Pritchard et al. 2017), all of which agree that the changes in fire regime over the past century are strongly associated with forest encroachment and densification. Research suggests that there was likely a temporal mixed-severity fire regime. During moderate or normal climate periods, there would be more frequent fire of variable intensity on the warmer and drier parts of the landscape (Brown 2006, Gedalof 2011, Rogeau 2016), maintaining grasslands, open-canopy forests, and patchy forest–meadow complexes. Driven by extreme (dry, hot, windy) climate conditions large severe fires would occur on occasion (such as the 1910 fires) and burn more indiscriminately across fuel types (Miller and Urban 2000, Peterson et al. 2005, Hessburg et al. 2016). It is difficult to prove that changes in fire regimes are directly responsible for the widespread losses of open grasslands and open-canopy woodlands because some of the same variables that drive variability in fire behavior (elevation and insolation) affect variability in vegetation. However, it is not difficult to see how wildfire suppression since the early- to mid-1900s has influenced vegetation succession patterns of the landscape (Cumming 2005, Pyne 2008).

The observed increases in tree cover could be partially attributed to changes in climate to conditions more favorable for tree establishment. An age-class analysis of new forests could provide further insight into this. A decrease in tree age with increasing distance from the forest edges in these new forests would suggest gradual

encroachment over time. However, if new forest patches are even-aged it would suggest a single pulse of establishment occurred over a large area. This could indicate that climate or seedbed conditions became favorable (Luckman et al. 1997, Edwards et al. 2008) or that a decline in disturbance occurred.

Grassland-to-forest conversion at lower elevations was also likely influenced by reductions in populations of elk, bison, and other ungulates since European settlement of the region (Campbell et al. 1994, Brink 2008, Painter et al. 2018). While the historical interactions between grazing, fire, and grassland–forest ecotones are complex (Bachelet et al. 2000, White 2001, White et al. 2003b), the reduced pressure on woody shrub and tree recruitment that results from the removal of fire, grazing, and trampling clearly pushes the ecotone in favor of forests (Nelson and England 1971, White et al. 2003b, Painter et al. 2018). Increased aspen recruitment in Yellowstone National Park and in Alberta has been directly linked to reductions in elk browsing due to declining populations (White et al. 2003b, Painter et al. 2018), and bison extirpation has been linked with forest encroachment into aspen parkland since the late 1800s in North America (Campbell et al. 1994). Bison effects on forest–grassland boundaries result from browsing, trampling, wallowing, and toppling (Campbell et al. 1994, Bork et al. 2013, Baraniewicz and Perzanowski 2015). Bison primarily browse graminoids (Plumb and Dodd 1993), but they also browse woody shrubs, and broadleaf deciduous and CF saplings (Leonard et al. 2017), which would limit forest expansion. We saw many large areas of young aspen stands in the 1913 photographs that may well date to the time of the bison extirpation.

This study applied new technology (Bozzini et al. 2012) and novel techniques (Stockdale et al. 2015) in oblique-image analysis to spatially and quantitatively assess landscape vegetation change from the beginning of European settlers' arrival in southwestern Alberta. To make the most effective use of historical oblique imagery, we advise the following: (1) limit the areas to be classified within the image to where vegetation categories can be clearly identified (i.e., restrict the viewshed); (2) rather than sequentially georeferencing and then classifying images to cover the landscape,

determine the best image to use to classify specific locations (proximity and angle of view); (3) classify the images at a finer resolution to enable more detailed measurements to be taken of the vegetation; (4) develop supervised classification methods unique to oblique imagery to enable analysis of larger collections of imagery (Fortin et al. 2018).

While our study showed that the majority of the landscape was in the same broad vegetation category in 2008 as it was in 1909, it is important to note the following caveats: (1) the closed-canopy coniferous forest category did not include changes in species composition or age class; (2) the grassland and meadow category did not differentiate between true grasslands and heavily grazed agricultural land, cropland, and human-maintained clearings; (3) the mixedwood category encompassed considerable variation in the ratio of broadleaf deciduous to coniferous trees; and (4) the open-canopy woodland category varied from grasslands intermingled with single or clustered large *Pseudotsuga menziesii* trees to talus slopes with krummholz to grassland with interspersed aspen copses. Furthermore, we likely have underestimated forest closure in general, given that oblique-image classification methods tend to under-represent open-canopy forests and small clearings.

Future climates in our study region are expected to drive vegetation change in the opposite direction to what we observed over the past century: The Foothills Fescue NSR vegetation type is expected to expand into what is now the Montane NSR, which in turn will expand into what is currently the Subalpine NSR, which in turn will encroach upon the Alpine NSR (Schneider 2013). Thus, it appears current vegetation may be less suited to climatic conditions than the historical vegetation would be. This aligns with Flatley and Fulé (2016), who found historical vegetation (from the 1900s) was better suited to projected climate change than the current vegetation. Some find forest expansion into grasslands and meadows to be concerning (Arno and Gruell 1983, Archer 1994, Noss 2013), as this threatens rangeland resources (Gruell 1983, Archer 1994), has substantial impacts on biodiversity of low-elevation grasslands (Haugo and Halpern 2010) and higher elevation subalpine/alpine meadows (Franklin et al. 1971), and may increase the risk

of intense wildfire (Stockdale et al. 2019). Others are less concerned with the long-term effects of such encroachment, arguing that we are in an interregnum of wildfire activity that will eventually catch up to remove much of the new forest (Weir et al. 1995) and restore the grassland–forest boundary to where it is most climatically suitable. Under future, suitable, climatic conditions large, severe wildfires are likely to occur in this area, as they did in the past (1910, 2003), burning back forests that have encroached into grasslands (Collins et al. 2009, Holden et al. 2010), depending on climate suitability these areas could remain as grassland into the future. This conversion of forest to grassland may occur just to the south of our study area near Waterton Lakes National Park, where a large, high-severity wildfire occurred in the late summer of 2017 (the Kenow fire), and a smaller fire burned through aspen stands at the northern end of the Bob Creek Wildland. However, given the complex feedbacks between climate, vegetation, and disturbance regimes (Krawchuk and Moritz 2011, Flatley and Fulé 2016), there is also the possibility that alternate-to-historical successional trajectories may result, producing the potential for novel ecosystems to emerge in the future (Hobbs et al. 2014).

This study has helped to elucidate the vegetation composition of the landscape at the turn of the twentieth century and could be used to guide restoration efforts and active management for ecological integrity (Jackson and Hobbs 2009). A major challenge associated with ecological restoration is determining what the appropriate reference conditions ought to be (Stephens and Fulé 2005, Higgs et al. 2014), and any such restoration plan must consider the many risks associated with such large-scale change. While historic vegetation structure might be suitable for projected future climate (Schneider 2013), and may reduce landscape-level wildfire risk (Stockdale et al. 2019), there is no guarantee that the vegetation structure would be stable over time given the interactions between vegetation, climate, direct human impacts, invasive species, and disturbance regime (Flatley and Fulé 2016). However, ecological restoration does not need to be the end goal to make historical analyses worthwhile. Understanding how the present landscape came to be as a result of past events

has intrinsic value in understanding landscape patterns and processes and can provide a foundation upon which to address management challenges.

## ACKNOWLEDGMENTS

Special thanks are due to Cat Boyes for diligent work in preparing the images used in this analysis, and Caitlin Mader and Margaret Raimann for compiling images and other data sets used in this work. Funding for this research came from a variety of sources including (1) a Natural Sciences and Engineering Research Council of Canada (NSERC) Postgraduate Doctoral Scholarship, (2) the University of Alberta, Presidents Award, (3) Alberta Innovates, Technology Futures Graduate Student Scholarship, (4) the University of Alberta, Queen Elizabeth II Doctoral Scholarship, and (5) an NSERC Discovery Grant to SEM. Our work depended on the digital collections of the Mountain Legacy Project (University of Victoria; mountainlegacy.ca), and in turn their partnership with Library and Archives Canada. The authors declare that there are no conflicts of interest with regard to this work.

## LITERATURE CITED

- Andison, D. W. 1998. Temporal patterns of age-class distributions on foothills landscapes in Alberta. *Ecography* 21:543–550.
- Archer, S. 1994. Woody plant encroachment into southwestern grasslands and savannahs: rates, patterns and proximate causes. Pages 13–68 in M. Vavra, W. Laycock, and R. Pieper, editors. *Ecological implications of livestock herbivory in the West*. Society for Range Management, Denver, Colorado, USA.
- Archibald, J., I. Corns, and G. Klappstein. 1996. Field guide to ecosites of southwestern Alberta. Special Report 8. Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta, Canada.
- Arno, S. F. 1980. Forest fire history in the northern Rockies. *Journal of Forestry* 78:460–465.
- Arno, S. F., and G. E. Gruell. 1983. Fire history at the forest-grassland ecotone in southwestern Montana. *Journal of Range Management* 36:332–336.
- Arno, S. F., D. J. Parsons, and R. E. Keane. 2000. Mixed severity fire regimes in the Northern Rocky Mountains: consequences of fire exclusion and options for the future. *USDA Forest Service Proceedings Rocky Mountain Research Station* 5:225–232.
- Bachelet, D., J. M. Lenihan, C. Daly, and R. P. Neilson. 2000. Interactions between fire, grazing and climate change at Wind Cave National Park, SD. *Ecological Modelling* 134:229–244.
- Baker, W. L. 1992. Effects of settlement and fire suppression on landscape structure. *Ecology* 73:1879–1887.
- Baraniewicz, M., and K. Perzanowski. 2015. Are reintroduced wisents a threat to mountain forests? *Annales Zoologici Fennici* 52:301–312.
- Barrett, S. W. 1996. The historic role of fire in Waterton Lakes National Park, Alberta. Contract report for Parks Canada.
- Barrett, S. W., and S. F. Arno. 1988. Increment-borer methods for determining fire history in coniferous forests. INT GTR-244, USDA. Forest Service, Intermountain Research Station, Ogden, Utah, USA.
- Barrett, S. W., D. Havlina, J. Jones, W. Hann, C. Frame, D. Hamilton, K. Schon, T. Demeo, L. Hutter, and J. Menakis. 2010. *Interagency Fire Regime Condition Class Guidebook*. Version 3.0. <https://www.frame.s.gov/catalog/7793>
- Beller, E., L. McClenachan, A. Trant, E. Sanderson, J. Rhemtulla, A. Guerrini, R. Grossinger, and E. Higgs. 2017. Toward principles of historical ecology. *American Journal of Botany* 104:645–648.
- Bergeron, Y., S. Gauthier, V. Kafka, P. Lefort, and D. Lesieur. 2001. Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. *Canadian Journal of Forest Research* 31:384–391.
- Bork, E., C. Carlyle, J. Cahill, R. Haddow, and R. Hudson. 2013. Disentangling herbivore impacts on *Populus tremuloides*: a comparison of native ungulates and cattle in Canada's Aspen Parkland. *Oecologia* 173:895–904.
- Bozzini, C., M. Conedera, and P. Krebs. 2012. A new monoploting tool to extract georeferenced vector data and orthorectified raster data from oblique non-metric photographs. *International Journal of Heritage in the Digital Era* 1:499–518.
- Bradley, C., and C. Wallace. 1996. *Prairie ecosystem management: an Alberta perspective*. Prairie Conservation Forum, Occasional Paper 2, Lethbridge, Alberta, Canada.
- Brink, J. 2008. *Imagining head-smashed-in: Aboriginal buffalo hunting on the northern plains*. AU Press, Edmonton, Alberta, Canada.
- Brown, P. M. 2006. Climate effects on fire regimes and tree recruitment in Black Hills ponderosa pine. *Ecology* 87:2500–2510.
- Brown, P. M., M. R. Kaufmann, and W. D. Shepperd. 1999. Long term, landscape patterns of past fire events in a montane ponderosa pine forest of central Colorado. *Landscape Ecology* 14:513–532.
- Campbell, C., I. Campbell, C. Blyth, and J. McAndrews. 1994. Bison extirpation may have caused aspen expansion in western Canada. *Ecography* 17:360–363.



- Carcaillet, C., Y. Bergeron, P. Richard, B. Frechette, S. Gauthier, and Y. Prairie. 2001. Change of fire frequency in the eastern Canadian boreal forests during the Holocene: Does vegetation composition or climate trigger the fire regime? *Journal of Ecology* 89:930–946.
- Collins, B. M., J. D. Miller, A. E. Thode, M. Kelly, J. W. van Wagtenonk, and S. L. Stephens. 2009. Interactions among wildland fires in a long established Sierra Nevada natural fire area. *Ecosystems* 12:114–128.
- Cumming, S. 2005. Effective fire suppression in boreal forests. *Canadian Journal of Forest Research* 35:772–786.
- Daniels, L. D., Z. Gedalof, and M. Pisaric. 2011. Historic climate-fire-vegetation interactions of the west versus east Kootenays: implications of climate change and fire suppression. Contract report for Foothills Research Institute.
- Dordel, J., M. Feller, and S. W. Simard. 2008. Effects of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) infestations on forest stand structure in the southern Canadian Rocky Mountains. *Forest Ecology and Management* 255:3563–3570.
- Edwards, T. W., S. J. Birks, B. H. Luckman, and G. M. MacDonald. 2008. Climatic and hydrologic variability during the past millennium in the eastern Rocky Mountains and northern Great Plains of western Canada. *Quaternary Research* 70:188–197.
- Ehle, D. S., and W. L. Baker. 2003. Disturbance and stand dynamics in ponderosa pine forests in Rocky Mountain National Park, USA. *Ecological Monographs* 73:543–566.
- Elliott, G. P. 2011. Influences of 20th-century warming at the upper tree line contingent on local-scale interactions. Evidence from a latitudinal gradient in the Rocky Mountains, USA. *Global Ecology and Biogeography* 20:46–57.
- Fichera, C. R. 2012. Land Cover classification and change-detection analysis using multi-temporal remote sensed imagery and landscape metrics. *European Journal of Remote Sensing* 45:1–18.
- Flatley, W. T., and P. Z. Fulé. 2016. Are historical fire regimes compatible with future climate? Implications for forest restoration *Ecosphere* 7:e01471.
- Fortin, J. A., J. T. Fisher, J. M. Rhemtulla, and E. S. Higgs. 2018. Estimates of landscape composition from terrestrial oblique photographs suggest homogenization of Rocky Mountain landscapes over the last century. *Remote Sensing in Ecology and Conservation*. <http://dx.doi.org/10.1002/rse2.100>
- Franklin, J. F., W. H. Moir, G. W. Douglas, and C. Wiberg. 1971. Invasion of subalpine meadows by trees in the Cascade Range, Washington and Oregon. *Arctic and Alpine Research* 3:215–224.
- Fuhlendorf, S. D., and D. M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. *BioScience* 51:625.
- Fulé, P. Z., W. W. Covington, M. M. Moore, T. A. Heinlein, and A. E. M. Waltz. 2002. Natural variability in forests of the Grand Canyon, USA. *Journal of Biogeography* 29:31–47.
- Fulé, P. Z., J. E. Crouse, A. E. Cocke, M. M. Moore, and W. Covington. 2004. Changes in canopy fuels and potential fire behavior 1880–2040: Grand Canyon, Arizona. *Ecological Modelling* 175:231–248.
- Gallant, A. L., A. J. Hansen, J. S. Councilman, D. K. Monte, and D. W. Betz. 2003. Vegetation dynamics under fire exclusion and logging in a Rocky Mountain watershed, 1856–1996. *Ecological Applications* 13:385–403.
- Gedalof, Z. 2011. Climate and spatial patterns of wildfire in North America. Pages 89–115 *in* D. McKenzie, C. Miller, and D. A. Falk, editors. *The landscape ecology of fire*. Springer Netherlands, Dordrecht, The Netherlands.
- Gruell, G. E. 1983. Fire and vegetative trends in the Northern Rockies: interpretations from 1871–1982 photographs. INT GTR-158, USDA. Forest Service, Intermountain Research Station, Ogden, Utah, USA.
- Hastings, J. R., and R. M. Turner. 1965. The changing mile. An ecological study of vegetation change with time in the lower mile of an arid and semiarid region. University of Arizona Press, Tucson, Arizona, USA.
- Haugo, R. D., and C. B. Halpern. 2010. Tree age and tree species shape positive and negative interactions in a montane meadow. *Botany-Botanique* 88:488–499.
- Hawkes, B. C. 1979. Fire history and fuel appraisal of Kananaskis Provincial Park. Thesis. University of Alberta, Edmonton, Alberta, Canada.
- Hessburg, P. F., and J. K. Agee. 2003. An environmental narrative of Inland Northwest US forests: 1800–2000. *Forest Ecology and Management* 178:23–59.
- Hessburg, P. F., J. K. Agee, and J. F. Franklin. 2005. Dry forests and wildland fires of the inland Northwest USA: contrasting the landscape ecology of the pre-settlement and modern eras. *Forest Ecology and Management* 211:117–139.
- Hessburg, P. F., B. Smith, R. B. Salter, R. D. Ottmar, and E. Alvarado. 2000. Recent changes (1930s–1990s) in spatial patterns of interior northwest forests, USA. *Forest Ecology and Management* 136:53–83.
- Hessburg, P. F., et al. 2016. Tamm Review: management of mixed-severity fire regime forests in Oregon, Washington and Northern California. *Forest Ecology and Management* 366:221–250.

- Heyerdahl, E. K., L. B. Brubaker, and J. K. Agee. 2001. Spatial controls of historical fire regimes: a multi-scale example from the Interior West, USA. *Ecology* 82:660–678.
- Heyerdahl, E. K., P. Morgan, and J. P. Riser. 2008. Multi-season climate synchronized historical fires in dry forests (1650–1900), northern Rockies, USA. *Ecology* 89:705–716.
- Higgs, E., G. Bartley, and A. Fisher. 2009. *The Mountain Legacy Project*. Second edition. University of Victoria Press, Victoria, British Columbia, Canada.
- Higgs, E., D. Falk, A. Guerrini, M. Hall, J. Harris, R. J. Hobbs, S. T. Jackson, J. M. Rhemtulla, and W. Throop. 2014. The changing role of history in restoration ecology. *Frontiers in Ecology and the Environment* 12:499–506.
- Hobbs, R. J., et al. 2014. Managing the whole landscape: historical, hybrid, and novel ecosystems. *Frontiers in Ecology and the Environment* 12:557–564.
- Holden, Z. A., P. Morgan, and A. T. Hudak. 2010. Fire severity of areas reburned by wildfires in the Gila National Forest, New Mexico, USA. *Fire Ecology* 6:77–85.
- Hughes, J., A. Fall, L. Safranyik, and K. Lertzman. 2006. Modelling the effect of landscape pattern on mountain pine beetles. Information Report BC-X-407. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia, Canada.
- Jackson, S. T., and R. J. Hobbs. 2009. Ecological restoration in the light of ecological history. *Science* 325:567–569.
- Johnson, E. A., and G. I. Fryer. 1987. Historical vegetation change in the Kananaskis Valley, Canadian Rockies. *Canadian Journal of Botany* 65:853–858.
- Johnson, E. A., K. Miyanishi, and H. Kleb. 1994. The hazards of interpretation of static age structures as shown by stand reconstructions in a *Pinus contorta* - *Picea engelmannii* forest. *Journal of Ecology* 82:923–931.
- Klasner, F. L., and D. B. Fagre. 2002. A half century of change in alpine treeline patterns at Glacier National Park, Montana, USA. *Arctic, Antarctic, and Alpine Research* 34:49–56.
- Krawchuk, M., and M. Moritz. 2011. Constraints on global fire activity vary across a resource gradient. *Ecology* 9:121–132.
- Kubian, R. 2013. Characterizing the mixed severity fire regime of the Kootenay Valley, Kootenay National Park. Thesis. University of Victoria, Victoria, British Columbia, Canada.
- Leonard, J., L. Perkins, D. Lammers, and J. Jenks. 2017. Are bison intermediate feeders? Unveiling summer diet selection at the northern fringe of historical distribution. *Rangeland Ecology and Management* 70:405–410.
- Luckman, B. H., K. R. Briffa, P. D. Jones, and F. H. Schweingruber. 1997. Tree-ring based reconstruction of summer temperatures at the Columbia Icefield, Alberta, Canada, AD 1073–1983. *Holocene* 7:375–389.
- Luckman, B., and T. Kavanagh. 2000. Impact of climate fluctuations on mountain environments in the Canadian Rockies. *AMBIO: A Journal of the Human Environment* 29:371–380.
- Lykke, A. M. 2000. Local perceptions of vegetation change and priorities for conservation of woody savanna vegetation in Senegal. *Journal of Environmental Management* 59:107–120.
- MacDonald, G., C. Larsen, J. Szeicz, and K. Moser. 1991. The reconstruction of boreal forest fire history from lake sediments: a comparison of charcoal, pollen, sedimentological, and geochemical indices. *Quaternary Science Reviews* 10:53–71.
- MacLaren, I. S. 2005. *Mapper of Mountains: M.P. Bridgland in the Canadian Rockies, 1902–1930*. University of Alberta Press, Edmonton, Alberta, Canada.
- McCaffrey, D. R., and C. Hopkinson. 2017. Assessing fractional cover in the alpine treeline ecotone using the WSL Monoplotting Tool and airborne Lidar. *Canadian Journal of Remote Sensing* 43:504–512.
- Miller, C., and D. L. Urban. 2000. Connectivity of forest fuels and surface fire regimes. *Landscape Ecology* 15:145–154.
- Moore, M. M., D. W. Huffman, P. Z. Fulé, W. W. Covington, and J. E. Crouse. 2004. Comparison of historical and contemporary forest structure and composition on permanent plots in southwestern ponderosa pine forests. *Forest Science* 50:162–176.
- Natural Regions Committee. 2006. *Natural Regions and Subregions of Alberta*. Compiled by D. J. Downing and W. W. Pettapiece. Publication T/852, Government of Alberta, Edmonton, Alberta, Canada.
- Nelson, J. G., and R. E. England. 1971. Some comments on the causes and effects of fire in the Northern Grasslands area of Canada and the nearby United States. C.A. 1750–1900. *Canadian Geographer* 15:295–306.
- Noss, R. F. 2013. *Forgotten grasslands of the south*. Island Press, Washington, D.C., USA.
- Painter, L., R. Beschta, E. Larsen, and W. Ripple. 2018. Aspen recruitment in the Yellowstone region linked to reduced herbivory after large carnivore restoration. *Ecosphere* 9:e02376.
- Parks, S. A., C. Miller, C. Nelson, and Z. Holden. 2014. Previous fires moderate burn severity of subsequent wildland fires in two large western US wilderness areas. *Ecosystems* 17:29–42.

- Peterson, D. L., M. C. Johnson, J. K. Agee, T. B. Jain, D. McKenzie, and E. D. Reinhardt. 2005. Forest structure and fire hazard in dry forests of the western United States. PNW-GTR-268. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Plumb, G. E., and J. L. Dodd. 1993. Foraging ecology of bison and cattle on a mixed prairie: implications for natural areas management. *Ecological Applications* 3:631–643.
- Prichard, S. J., P. Hessburg, R. Gray, N. Povak, B. Solter, C. Stevens-Rumann, and P. Morgan. 2018. Final Report: evaluating the influence of prior burn mosaics on subsequent wildfire behavior, severity, and fire management options. Joint Fire Science Project 14\_1\_02\_30.
- Prichard, S. J., C. S. Stevens-Rumann, and P. F. Hessburg. 2017. Shifting global fire regimes: lessons from reburns and research needs. *Forest Ecology and Management* 396:217–233.
- Pyne, S. J. 2008. *Awful splendour. A fire history of Canada*. UBC Press, Vancouver, British Columbia, Canada.
- Quigley, T. M., S. J. Arbelbide, technical editors. 1997. An assessment of ecosystem components in the interior Columbia basin and portions of the Klamath and Great Basins: volume 1. PNW-GTR-405. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Rhemtulla, J. M., R. J. Hall, E. S. Higgs, and S. E. Macdonald. 2002. Eighty years of change: vegetation in the montane ecoregion of Jasper National Park, Alberta, Canada. *Canadian Journal of Forest Research* 32:2010–2021.
- Rogeanu, M.-P. 1999. Fire history study of the Central Rockies Ecosystem Inter-Agency North-Saskatchewan Unit. Contract report for CREIL Members: Parks Canada, the Alberta Land and Forest Service and, Alberta Provincial Parks., Banff, Alberta, Canada.
- Rogeanu, M.-P. 2016. Fire regimes of southern Alberta, Canada. Dissertation. University of Alberta, Edmonton, Alberta, Canada.
- Romme, W. H., et al. 2009. Historical and modern disturbance regimes, stand structures, and landscape dynamics in piñon–juniper vegetation of the western United States. *Rangeland Ecology and Management* 62:203–222.
- Schneider, R. R. 2013. Alberta's Natural Subregions under a changing climate: past, present and future. Alberta Biodiversity Monitoring Institute. <http://www.abmi.ca/home/publications/251-300/291.html;jsessionid=1697AE40BDADC9852A654DFEADA0E575?mode=detail&time=2013>
- Shaw, A. K. 2009. Conservation and ecological restoration of Rocky Mountain subalpine meadows: vegetation responses to tree encroachment. Thesis. University of Victoria, Victoria, British Columbia, Canada.
- Stephens, S., and P. Fulé. 2005. Western pine forests with continuing frequent fire regimes: possible reference sites for management. *Journal of Forestry* October/November: 357–362.
- Stockdale, C. A. 2017. A century of landscape change in the southern Rocky Mountains and foothills of Alberta: using historical photography to quantify ecological change. Dissertation. University of Alberta, Edmonton, Alberta, Canada.
- Stockdale, C. A., C. Bozzini, S. E. Macdonald, and E. Higgs. 2015. Extracting ecological information from oblique angle terrestrial landscape photographs: performance evaluation of the WSL Monoplotting Tool. *Applied Geography* 63:315–325.
- Stockdale, C. A., N. McLoughlin, M. Flannigan, and S. E. Macdonald. 2019. Could restoration of a landscape to a pre-European historical vegetation condition reduce burn probability? *Ecosphere* 10: e02584.
- Strong, W. L. 1977. Pre- and postsettlement palynology of southern Alberta. *Review of Palaeobotany and Palynology* 23:373–387.
- Tande, G. F. 1979. Fire history and vegetation patterns of coniferous forests in Jasper National Park, Alberta. *Canadian Journal of Botany* 57:1912–1931.
- Trant, A., B. Starzomski, and E. Higgs. 2015. A publicly available database for studying ecological change in mountain ecosystems. *Frontiers in Ecology and the Environment* 13:187.
- Van Wagner, C. E., M. Finney, and M. Heathcott. 2006. Historical fire cycles in the Canadian Rocky Mountain Parks. *Forest Science* 52:704–717.
- Watt-Gremm, G. 2007. Taking a good long look: disturbance, succession, landscape change and repeat photography in the upper Blakiston Valley, Waterton Lakes National Park. Thesis. University of Victoria, Victoria, British Columbia, Canada.
- Webb, R. H. 1996. A century of environmental change in Grand Canyon. Repeat photography of the 1889–1890. University of Arizona Press, Tucson, Arizona, USA.
- Weir, J. M. H., K. J. Chapman, and E. A. Johnson. 1995. Wildland fire management and the fire regime in the southern Canadian Rockies. INT GTR-320. USDA Forest Service, Intermountain Research Station, Ogden, Utah, USA.
- White, C. 2001. Aspen, elk, and fire in the Canadian Rocky Mountains. Dissertation. University of British Columbia, Vancouver, British Columbia, Canada.
- White, C., M. Feller, and S. Bayley. 2003b. Predation risk and the functional response of elk-aspen



- herbivory. *Forest Ecology and Management* 181: 77–97.
- White, C., I. Pengelly, D. Zell, and M.-P. Rogeau. 2003a. Landscape fire regimes and vegetation restoration in Banff National Park, Alberta. Occasional Paper BNP-2003-01. Parks Canada, Banff, Alberta, Canada.
- Wimberly, M. C., and R. S. Kennedy. 2008. Spatially explicit modelling of mixed-severity fire regimes and landscape dynamics. *Forest Ecology and Management* 254:511–523.
- Wright, C. S., and J. K. Agee. 2004. Fire and vegetation history in the eastern Cascade Mountains, Washington. *Ecological Applications* 14:443–459.

## SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2774/full>