



A tale of two disturbances: can mountain pine beetle restore landcover composition and pattern altered by fire suppression in Jasper National Park?

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Abstract

Disturbance is a key driver of heterogeneity in mountain landscapes. Historically, the montane ecoregion (i.e., lower elevations where the climate is typically warmer and drier) in Jasper National Park experienced a mixed-severity fire regime with short fire return intervals. However, fire suppression over the previous century has altered the fire return interval, resulting in a significant increase of homogenous forest cover. These changes contributed to an extensive mountain pine beetle (MPB; *Dendroctonus ponderosae*) outbreak in the park over the previous decade, which impacted up to 90% of lodgepole pine (*Pinus contorta*). With no previous records of MPB in the park, new research is required to investigate whether the composition and pattern of ecosystems in the montane ecoregion have departed from their historical range of variability due to altered or novel disturbance. In this study, we compare the composition and pattern of landcover in the aftermath of historical, stand-replacing fires (1889 and 1905) and the recent MPB outbreak. We repeated historical survey photographs (captured in 1915) and employed a recently developed workflow for classifying and georeferencing oblique images to produce historical and contemporary landcover maps for a study area in the montane ecoregion. Our results indicate that the MPB outbreak has reduced the area-weighted mean patch size for mature conifer and increased patch complexity in our study area. We conclude that MPB has reintroduced heterogeneity to the montane ecoregion, but also acknowledge that succession in MPB-affected stands will likely differ from post-fire disturbance as the insect only affects pine species. The timing of new compounding disturbances will further influence the recovery and future composition of species in the study area.

Keywords Jasper National Park · Repeat photography · Oblique image analysis · Historical range of variability · Landcover change · Novel disturbance

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Introduction

At the turn of the twentieth century, the central valleys of Jasper National Park (hereafter “Jasper NP”) in Alberta, Canada, were recovering from pervasive disturbance. Dendrochronological records indicate large, moderate-to-high severity wildfires burned through the area in 1889 and 1905 (Chavardès and Daniels 2016; Tande 1979). Consequently, this montane ecosystem was characterized by a patchy mosaic of regenerating forest and shrub, interspersed with open, mature forest, and myriad lakes, wetlands, and rivers. This landcover mosaic is evident in hundreds of photographs captured from survey stations above the valleys by the Dominion Lands Survey (DLS) in 1915 (Fig. 1). Eighty years later, Rhemtulla et al. (2002) repeated the original DLS survey photographs and developed a quantitative method to assess vegetation change between the image pairs.

Fig. 1 Top: Historical DLS survey photograph captured in 1915 from the Power House Cliff survey station in Jasper NP. Middle: Repeat photograph captured in 1998. Bottom: Second repeat photograph captured in 2019. Source: Mountain Legacy Project <https://explore.mountainlegacy.ca/stations/show/812>



The results indicated a significant increase in forest cover dominated by coniferous species (Fig. 1). The vegetation changes were attributed to a decrease in fire frequency and the authors forewarned that Jasper NP's maturing, even-aged forest stands were susceptible to future insect disturbance. Indeed, over the next decade, an outbreak of mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins) erupted in the park, impacting up to 90% of lodgepole pine (*Pinus contorta*) and rendering large swaths of forest with a telltale reddish hue (Fig. 1).

Disturbance is a key driver of ecosystem dynamics and can be defined as "any relatively discrete event that disrupts the structure of an ecosystem, community, or population, and changes resource availability or the physical environment" (White and Pickett 1985). This disruption changes the trajectory of an ecosystem and is fundamental in maintaining spatial and temporal heterogeneity evident at broader scales (Turner 2010). Natural disturbances occur over a range of time periods, and may be abiotic or biotic in origin, or a combination of the two (Turner 2010). A disturbance regime refers to the cumulative effects of a reoccurring disturbance agent over space and time (Keane 2013). Climate has a strong influence on many disturbance regimes, affecting their intensity, severity, frequency, extent, and duration (Seidl et al. 2020). Over time, the bounds of ecosystem variability become defined as species adapt to reoccurring disturbance. The concept *historical range of variability* characterizes the conditions between these bounds, providing a sense of the range of ecosystem characteristics exhibited in response to disturbance and recovery over time and space (Keane et al. 2009; Landres et al. 1999; Morgan et al. 1994).

In the Canadian Rockies, fire is recognized as a primary disturbance agent influencing forest dynamics, but insects, pathogens, floods, avalanches, and windstorms also play a role (Luckman 1998; Wright and Heinselman 1973). Wildfires occur both via lightning strikes and anthropogenic sources. Historically, Indigenous peoples have used fire for a variety of uses, including to maintain travel routes and create forage to attract wildlife, and there is some evidence that the historic fire regime in Jasper NP was fueled primarily by human ignition (Lewis and Ferguson 1988; Murphy 2007; Turner 1999). Lodgepole pine (*Pinus contorta* var. *latifolia*), the dominant coniferous species in the montane ecoregion, is a fire-adapted/dependant species (Brown 1975). Mixed-severity and stand-replacing fires support spatial complexity and diverse species and age groups across the landscape.

However, montane ecosystems in the Canadian Rockies may have departed from their historical range of variability (HRV) due to the influence of altered and novel disturbance regimes. Fire return intervals (i.e., time between fires occurring on a landscape) have increased due to the effectiveness of pervasive fire exclusion (Keane et al. 2002). As visitation surged in the Canadian Rocky Mountain Parks after the

Second World War, fire was viewed as a threat to wilderness values (Woodley 1995). Park managers made use of new equipment, constructed fire roads, and installed fire tower networks to greatly improve fire suppression responses over the ensuing decades (Keane et al. 2002; Woodley 1995). Consequently, the buildup of hazardous fuels ultimately made it more difficult to fight fires. This issue has been exacerbated by climate warming which has lengthened fire seasons, decreased fuel moisture content, and increased natural ignitions, fire spread rates, fuel availability, and flammability (Seidl et al. 2017).

Altered fire regimes and climate warming in the Canadian Rockies have also created ideal conditions for MPB population growth. Native to western North American forests, MPB are innocuous in low numbers but under favorable conditions they can erupt to epidemic levels and attack mature pine species over vast areas (Safranyik and Carroll 2006). MPB outbreaks have occurred in mountain National Parks in the southern Canadian Rockies over the previous century but there are no records of the insect in Jasper NP prior to 1999 (Dalman 2004). However, a century of fire exclusion has resulted in a buildup of mature even-aged stands of lodgepole pine throughout the park's montane ecoregion. Additionally, the cold winter temperatures in the Canadian Rockies that limited the range of MPB have become more erratic with milder winters increasing overwintering survival of MPB broods (Cooke and Carroll 2017). These factors (abundance of host trees and mild winter temperatures) were the catalyst for a massive MPB outbreak beginning in central British Columbia in the late 1990s. Through long-range dispersal, the insect rapidly expanded beyond their historical range into central and northern Alberta, where evolutionary naïve pine forests are more susceptible to MPB impacts (Burke et al. 2017; Cudmore et al. 2010; de lay Giroday et al. 2012; Raffa et al. 2008; Robinson 2015). The expansion of MPB into new habitats where they have not been present historically is an example of novel disturbance (Lieffers et al. 2023; Turner and Seidl 2023).

Altered and novel disturbances can drive changes in ecosystem composition and configuration, resulting in departures from their HRV. In Jasper NP, the historical and repeated survey photographs depict montane landcover in the aftermath of two extensive disturbance events. However, the recent MPB outbreak in the park is historically unprecedented and raises important questions about whether the characteristics of this event are within the HRV of the montane ecosystems.

The focus of this study is to compare the composition and pattern of the montane ecosystems after the two disturbance events to better understand what impact the novel insect disturbance imparted on landcover in Jasper NP's montane ecoregion. To undertake this comparison, we employ a recently developed workflow for classifying and

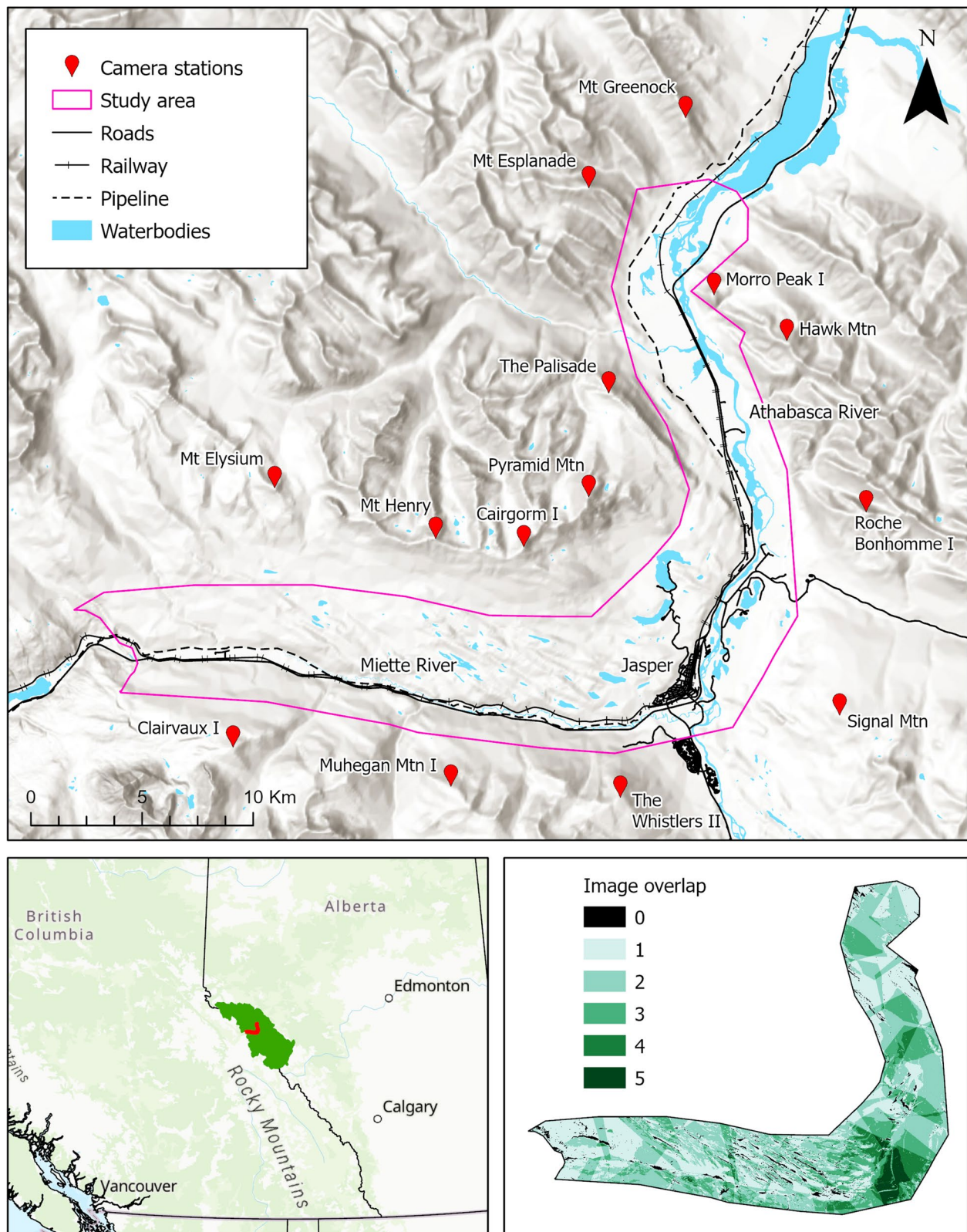


Fig. 2 Map of the study area (top panel) in Jasper National Park showing the survey stations (red pins) from which historical and repeat photographs were taken. The town of Jasper is located in the middle of the study area. Bottom left panel shows the location of the study area (red) in Jasper National Park (green) in Western Canada. Bottom right panel shows number of overlapping images across the study area

georeferencing oblique images to produce historical (1915) and contemporary (2020–2022) landcover maps for a study area in Jasper NP (Tricker et al. 2024). We use these two maps to assess the landcover changes that have occurred in the park since fire suppression began. We then overlay MPB extent data onto the contemporary map to assess the degree to which the MPB outbreak might be analogous to historic fire. We use this analysis to consider whether novel insect disturbance can reintroduce landcover composition and pattern altered by fire suppression in Jasper NP's montane ecoregion.

Study area

The study area comprises 26,424 hectares of the Miette and Athabasca River valleys in Jasper NP, located in the eastern Canadian Rockies in west-central Alberta (Fig. 2). This constitutes much of the lower elevation region of the park, where major national transportation routes and the town of Jasper are located. The park was established in 1907 and extends over 11,000 km². The steep elevational gradient in the park has a strong influence on the local climate and vegetation, resulting in three distinct ecoregions (Holland and Coen 1983). The lowest elevations comprise the montane ecoregion (1000–1350 m), where the climate is typically drier and warmer (Holland and Coen 1983). Lodgepole pine is the dominant tree species, although Douglas Fir (*Pseudotsuga menziesii*), white spruce (*Picea glauca*), and trembling aspen (*Populus tremuloides*) are also present (Holland and Coen 1983). Grasslands are interspersed among woodlands in the montane ecoregion, and wetlands are often found adjacent to water bodies (Beschta and Ripple 2007). The subalpine (1350–2300 m) and alpine (> 2300 m) ecoregions occupy the higher elevations in the park, where the climate is colder and wetter (Holland and Coen 1983). The mid-elevation subalpine ecoregion typically comprises subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and lodgepole pine forests, transitioning into open shrub-forb meadows in the high-elevation alpine ecoregion (Bradley and Neufeld 2012).

Dendrochronological analyses in the montane forests (that overlap with the present study area) indicate that historically Jasper NP experienced a mixed-severity fire regime with short fire return intervals. A study by Tande (1979) examined a 43,200 ha area centered on the town of Jasper and found evidence of 46 fires that burned between 1665 and 1913 (mean fire return interval of 5.5 years), most of which were low to medium intensity. A more recent study by Chavardès and Daniels (2016) assessed a 2000 ha area located 12 km north of the town of Jasper, revealing evidence of 13 mixed-severity fires between 1646 and 1905 (mean fire return interval of 20 years). Both studies found

evidence of widespread (i.e., > 50% of study area), medium to high intensity fires, which had a mean fire return interval of approximately 65 years. The most recent of these widespread fires occurred in 1889 (Tande 1979) and 1905 (Chavardès and Daniels 2016), with the former affecting up to 21% of the total area of Jasper NP (Luckman 1998). Both studies confirm that the fire regime and successional dynamics in the montane ecoregion have been substantially altered in the twentieth century due to fire exclusion.

Methods

We use a new workflow to classify and georeference historical and contemporary oblique photographs to produce 1915 and 2020/22 landcover maps for the study area in Jasper NP. We evaluate changes in the composition and pattern of the two maps that contributed to the extensive MPB outbreak that began in the park around 2010. We then assess the impact of the MPB outbreak on landcover composition and pattern in the 2020/22 map and compare these changes to the landcover depicted in the 1915 map.

The workflow for producing landcover data from oblique photographs was developed by researchers associated with the Mountain Legacy Project (<https://mountainlegacy.ca/>; Tricker et al. 2024). It incorporates two tools for classifying and georeferencing oblique images. The Python Landscape Classifier (PyLC; <https://github.com/scrose/pylc>) is a deep learning segmentation network trained on historical and repeat MLP images and their corresponding landcover classifications (Fortin et al. 2018; Jean et al. 2015; Rose 2020). PyLC classifies images into 9 landcover classes, which are based on the broad habitat types found in the Canadian Rockies (Table 1). The Image Analysis Toolkit (IAT; Sanseverino et al. 2016) georeferencing tool uses a web-based ray tracing algorithm to relate an image's field of view (FOV) to its geographic location using camera metadata (i.e., the camera location, azimuth, and FOV width) and a digital elevation model. Tricker et al. (2024) recently tested the accuracy of a landcover map produced from 19 oblique images using the workflow, reporting an average root-mean-square error of 4.6 m for georeferencing accuracy and 68% overall classification accuracy for the landcover map.

The historical survey photographs used in this analysis were captured by a DLS team led by Morrison Bridgland in 1915. The surveyors captured a total of 735 photographs on 4×6 inch glass plates from a network of 92 survey stations located predominantly on peaks and promontories above the three major valleys in the park. The glass plates were eventually stored at Libraries and Archives Canada (LAC) after Bridgland had used the images and theodolite measurements to produce topographical maps for the central portion of Jasper NP. To select images for inclusion in our analysis,

Table 1 Description of landcover classes used for classifying the historical and repeat images

Landcover classes	Description
Mature conifer	Greater than 75% mature coniferous trees
Broadleaf/mixed wood forest	> 70% broadleaf trees/patches with 30–70% broadleaf cover and the rest coniferous trees and/or shrub
Regenerating conifer	Young coniferous forest which is distinguishable from taller mature coniferous forest
Recently burned	Visibly recently burned forest
Shrub	> 25% shrub cover
Herbaceous	Forb-grassland < 25% shrub cover
Wetland	Vegetation with a wet or aquatic moisture regime
Water	Lakes and rivers
Barren ground	Soil, sand, gravel, rock, or anthropogenic impervious surfaces

we produced viewsheds for each image in ArcGIS Pro 3.0.2 (ESRI 2022) using the survey station coordinates and the image azimuths recorded by Rhemtulla et al. (2002) and a composite 2 m digital surface model. We developed digital surface and terrain models (DSM and DTM) for the study area using elevation data from Natural Resources Canada (2021) and airborne LiDAR data obtained from Jasper NP. We identified all images that had a viewshed footprint in the montane ecoregion of the Athabasca and Miette River valleys, and further refined this selection by assessing the quality (i.e., exposure and clarity) of each image. This left a final selection of 26 images captured from 14 survey stations, which provided 97.1% coverage of the study area (Online resource 1; Fig. 2). We obtained high-resolution scans (1600 dpi) of the historical images from LAC.

We undertook fieldwork in Jasper NP in the summers of 2020 and 2022 to capture repeat photographs of the 1915 images. We used a 51.4-megapixel FujiFilm GFX50s medium format digital camera with a 32–64-mm F4 zoom lens, and a custom-configured Novoflex panoramic head and tripod and followed protocols developed by the MLP (Fortin et al. 2018). This involved using gridded printouts of the original photographs to finetune the tripod position and align each repeat photograph through the camera's electronic viewfinder. We also recorded detailed field notes, including the camera location coordinates with an EOS Arrow 100 submeter GNSS receiver and the image azimuth with a Brunton transit. We visited all 14 survey stations and captured a total of 127 repeat photographs. These images were then uploaded to MLP Explorer—a map-based tool developed by the MLP for storing and viewing digital copies of the historical and repeated survey photographs in the MLP collection (<https://explore.mountainlegacy.ca/>).

The historical and repeat images were classified into the 10 landcover classes listed in Table 1 using PyLC. Manual corrections were undertaken in Affinity Photo Version 2.3.0 to improve classification accuracy for all landcover classes and remove tiling artifacts introduced by PyLC. We did not

classify beetle-killed forest given the difficulty of determining the extent and percent mortality in the repeat images. The 26 classified image pairs were then georeferenced using the IAT georeferencing tool following the steps outlined in Tricker et al. (2024). All classified images were georeferenced at 2 m resolution (i.e., the same resolution as the elevation datasets). To produce the historical (1915) and repeat (2020/22) landcover maps, the overlapping georeferenced classifications were combined using the majority value (i.e., the value that occurs most often) in ArcGIS Pro 3.0.2 with the cell statistics tool (ESRI 2022). This provided coverage for 92.3% of the study area (the remaining area had multiple majority values). To fill in the remaining areas, we followed an approach described by Tricker et al. (2024) involving iteratively dropping individual georeferenced classifications and recalculating the majority value until only one georeferenced classification remained. The resulting majority value grids were then mosaicked together using the Mosaic to New Raster, which brought the overall mapping coverage up to 97.1% (ESRI 2022). Finally, we used the Nibble tool to fill in the remaining gaps based on the nearest neighbor values (ESRI 2022).

We obtained 30-cm RGBI aerial imagery (captured in 2020) from Jasper NP to assess the accuracy of the 2020/22 landcover map. We generated 400 equalized stratified random points in ArcGIS Pro 3.0.2, which accounts for class imbalances by producing the same number of random points for each landcover class (ESRI 2022). We visually interpreted landcover from the aerial imagery at each random point, and constructed a confusion matrix to determine the overall, user's, and producer's accuracy of the 2020/22 landcover map. To assess landcover changes between the 1915 and 2020/22 maps, we calculated the area and percentage for the landcover classes in each map. We then used the Compute Change tool in ArcGIS Pro 3.0.2 to determine the spatial extent of the categorical changes between the two maps, with a focus on classes that converted to mature conifer in the 2020/22 landcover map (ESRI 2022). To determine changes in landcover pattern in the study area, we first used

the focal statistics tool in ArcPro 3.0.2 to apply a 10×10 cell neighborhood to the maps using the majority statistic to remove mosaicking artifacts, then calculated the area-weighted mean (i.e., each class is weighted by its proportional area in the study area) for the shape index (a measure of patch complexity) and patch size for each landcover class using Fragstats 4.2 (ESRI 2022; McGarigal et al. 2012).

Finally, to determine the amount of mature conifer impacted by MPB in the 2020/22 landcover map, we obtained the 2022 Vegetation Resources Inventory (VRI) dataset from Jasper NP (Government of British Columbia 2022). We used this dataset because PyLC is unable to distinguish live from dead canopy cover. We selected all polygons that were impacted by MPB by querying the disturbance join table. The Disturbance Percent Code for each selected polygon provides an estimate of percent basal area (or volume) of MPB-caused mortality, summarized in 10% bins (Fig. 3). We used these data to determine which areas of the 1915 landcover map would go on to be impacted by all MPB mortality bins in the future. We also used the 31–100% bins (i.e., moderate to high MPB severity) to determine which areas of mature conifer will likely undergo

changes in the 2020/22 landcover map. We recalculated the area and percentage of the adjusted landcover in ArcGIS Pro 3.0.2 and the area-weighted mean shape index and patch size in Fragstats 4.2 (ESRI 2022; McGarigal et al. 2012).

Results

The predominant landcover class in the 1915 landcover map is regenerating conifer (56.4% or 14,896.7 hectares) and is found throughout the western portion of the study area and along the western flanks of the northern portion (Table 2; Fig. 4). The second largest class is mature conifer (20.1%), with large stands present to the west of the study area along the Miette River and around Jasper townsite. Large stands of mature conifer are also present east of the Athabasca River in the central portion of the study area, and on the western flanks of the upper northern portion. Smaller stands of mature conifer are found adjacent to the Athabasca River throughout the northern portion. The main areas of shrub (10.4%) are located east of the Athabasca River and the northern corner of the study area. Water, comprising rivers

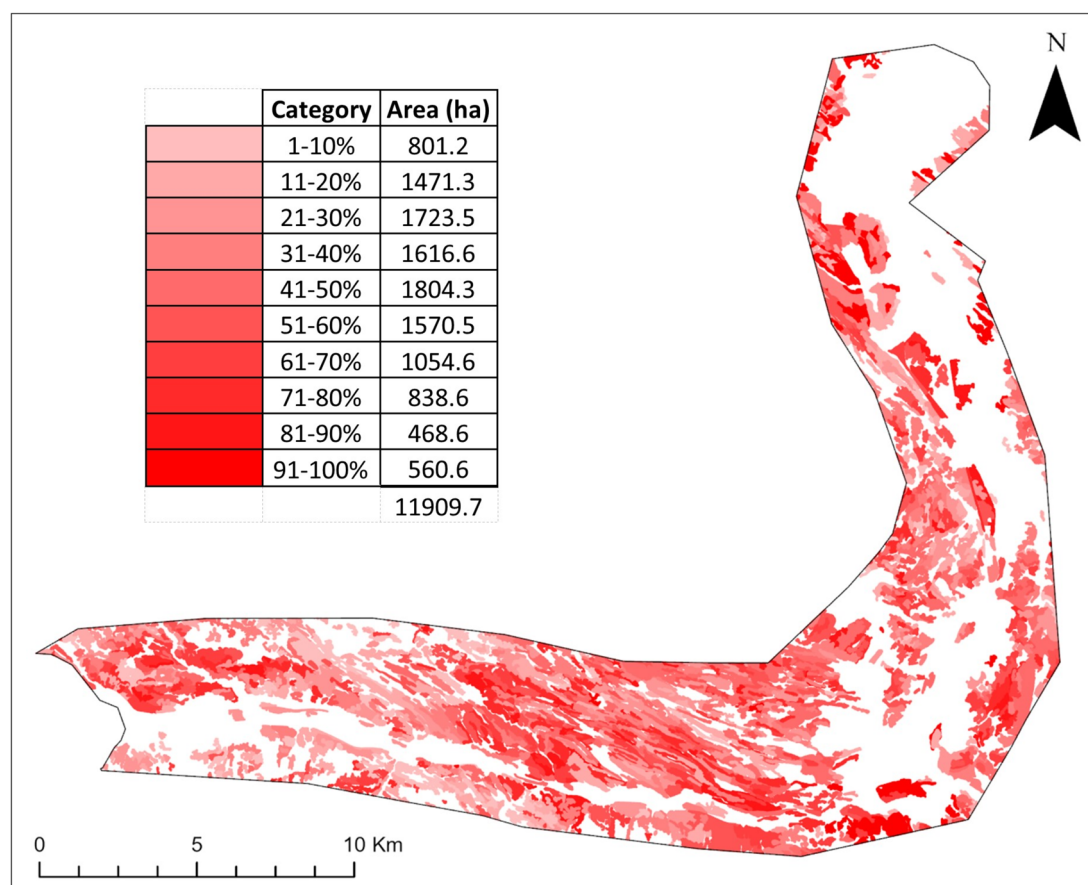


Fig. 3 Extent of MPB mortality in the Jasper NP study area. Mortality is an estimate of the percent basal area of dead trees in each polygon, summarized into 10% bins. Source: Government of British Columbia 2022

Table 2 Area and percentage of landcover classes for the 1915, 2020/22, and MPB-adjusted 2020/20 landcover maps

Landcover class	1915 map				2020/22 map				MPB-adjusted 2020/22 map			
	Area (ha)	%	Area-weighted mean shape index	Area-weighted mean patch size (ha)	Area (ha)	%	Area-weighted mean shape index	Area-weighted mean patch size (ha)	Area (ha)	%	Area-weighted mean shape index	Area-weighted mean patch size (ha)
Mature conifer	5308.9	20.1	5.62	226.5	21854.7	82.7	18.01	15228.0	14209.1	53.8	23.69	6381.8
Broadleaf/mixed wood	118.7	0.4	2.11	6.4	637.2	2.4	2.77	17.8	640.9	2.4	2.78	17.8
Regenerating conifer	14896.7	56.4	25.91	10968.2	52.7	0.2	2.95	3.6	52.7	0.2	2.95	3.6
MPB-affected conifer	0.0	0.0	0.00	0.0	0.0	0.0	0.00	0.0	7630.5	28.9	6.66	393.7
Recently burned	100.3	0.4	2.62	14.7	0.0	0.0	0.00	0.0	0.0	0.0	0.00	0.0
Shrub	2748.4	10.4	5.94	178.5	684.0	2.6	3.08	16.8	686.0	2.6	3.08	16.8
Herbaceous	583.6	2.2	5.39	213.1	640.1	2.4	3.77	49.4	642.3	2.4	3.77	49.4
Wetland	482.0	1.8	3.92	32.1	536.8	2.0	3.06	19.8	537.4	2.0	3.07	19.8
Water	1280.0	4.8	7.76	206.7	1206.4	4.6	8.46	202.7	1207.4	4.6	8.46	202.6
Barren ground	905.6	3.4	3.80	14.0	812.6	3.1	5.89	65.8	818.0	3.1	5.90	65.5

and lakes, makes up 4.8% of the study area. Barren ground (3.4%) comprises sand bars located along river courses, bands of rock in upper elevations of the northern portion of the study area and among the benchlands of the western portion, and roads and railways in the valley bottoms. Most of the herbaceous cover (2.2%) is located to the west of the Athabasca River and in small pockets within the Jasper townsite and toward the northern extent of the study area. This is also where a majority of wetlands (1.8%) are located, along with smaller areas along the Miette toward the western entrance of the park. Broadleaf/mixed wood forest (0.4%) and recently burned areas (0.4%) are the smallest classes, with former found in small stands throughout the study area and the latter located in upper elevations north of the Miette River. Regenerating conifer had the highest area-weighted mean shape index (25.91) and the largest area-weighted mean patch size (10,968.2 ha).

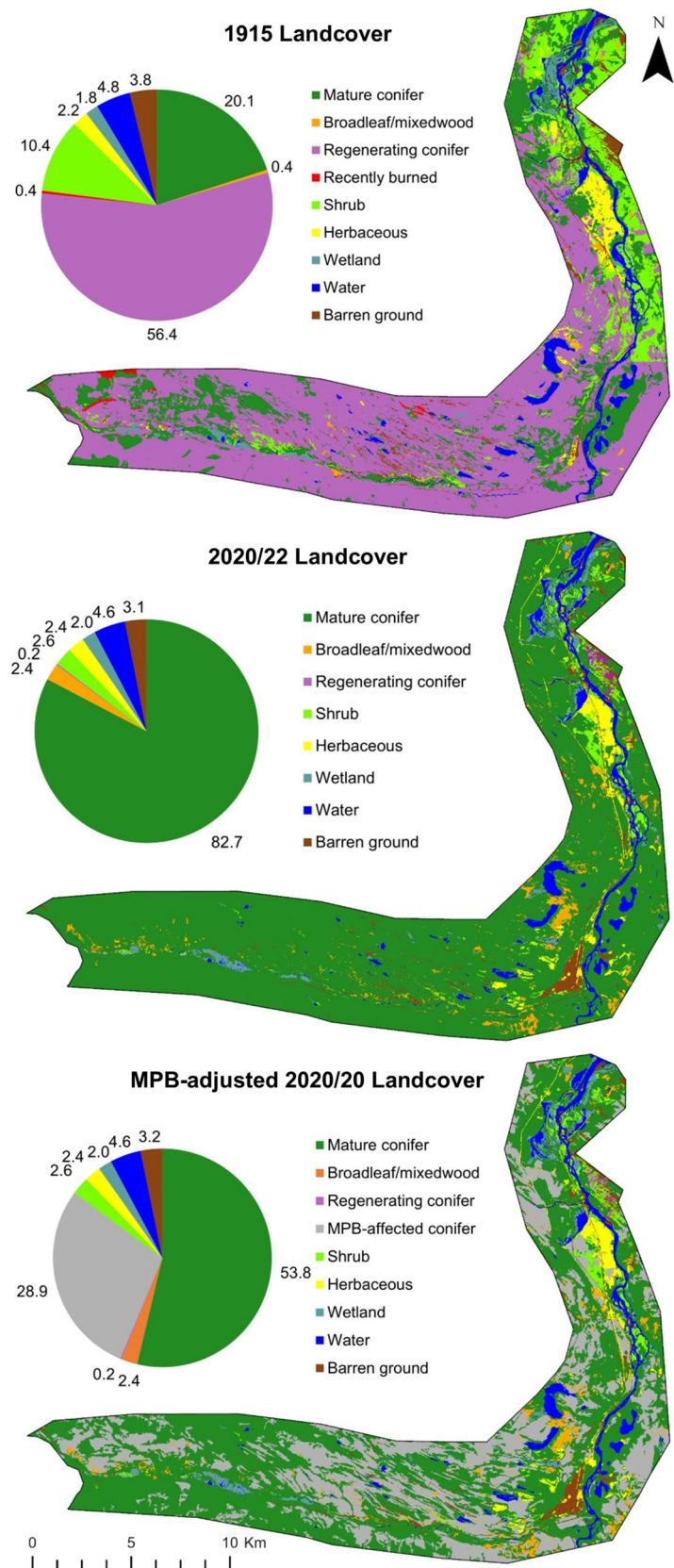
The 2020/22 landcover map is dominated by the mature conifer class (21,854.7 hectares), which now comprises 82.7% of the study area (Table 2; Fig. 4). Water (4.6%) is the next largest class, followed by barren ground (3.1%). Water is largely found in the same locations as the 1915 landcover map, but barren ground has decreased in upper elevations and gained area in the valley floor due to an increase in anthropogenic features and infrastructure, especially around the town of Jasper (Table 2). Shrub has decreased to 2.6% and is mostly found in the northern portion at lower elevations but also on the benchlands northwest and west of Jasper townsite. Stands of broadleaf/mixed wood forest (2.4%) have increased throughout the study area,

specifically in areas north, southwest, and southeast of the town, and along the eastern flanks of the northern portion. Herbaceous cover (2.4%) increased slightly despite the large area of grassland decreasing in the northern portion of the study area, with new areas emerging west, north, and east of the town. Wetland (2.0%) also increased slightly and is found largely in the same areas as the 1915 landcover map. The regenerating conifer class (0.2%) decreased significantly and is only found on the eastern flanks of the northern portion of the study area. There are no recently burned areas in the 2020/22 landcover map. Mature conifer had the highest area-weighted mean shape index (18.01) and the largest area-weighted mean patch size (15,228 ha).

The overall accuracy of the 2020/22 landcover map was 79% (Online resource 2). Water and herbaceous (both 94%) scored highest for user accuracy (i.e., the probability that features on the map is present on the ground). Mature conifer (80%) saw some confusion with broadleaf/mixed wood forest (74%), and vice versa. The lowest score was for barren ground (64%), which was confused with mature conifer, water, and shrub. The highest scores for producers' accuracy (i.e., the probability that features on the ground are correctly shown on the map) were regenerating conifer (97%), herbaceous (96%), and wetland (91%). Shrub (59%) was regularly confused with regenerating conifer, and mature conifer (65%) was misclassified as broadleaf/mixed wood forest or barren ground.

The change analysis showed that a majority of the historical landscape (16,958 ha, 64.2%) transitioned to mature conifer cover in 2020/22 (Table 3; Fig. 5). Most of the new

Fig. 4 The 1915 (top) and 2020/22 (middle) landcover maps derived from the historical and repeat photographs. The MPB-adjusted 2020/22 map (bottom) reflects mature conifer affected by moderate to high MPB severity. The pie charts depict the percent of landcover for each map



mature conifer cover originated from regenerating conifer (13,740.6 ha, 92.7%), followed by shrub (2011.6 ha, 73.2%). Almost all regenerating area (101.5 ha, 99.9%) transitioned to mature conifer, followed by barren ground (508.6 ha, 52.7%), broadleaf/mixed wood forest (80 ha, 67.1%), and herbaceous (219.5 ha, 37.9%). Table 4 indicates the area (ha) and percent of classes in the 1915 landcover map that would be impacted by MPB (using all mortality bins) a century later. This includes non-forest classes in 1915 that transitioned to forest classes in 2020/22.

The MPB-adjusted 2020/22 landcover map shows that MPB-affected conifer (7630.5 ha) comprises 28.9% of the study area (Table 2; Fig. 4). These changes occur at the

expense of mature conifer, which decreases from 21,854.7 ha (82.7%) to 14,209.1 (53.8%). Mature conifer had the highest area-weighted mean shape index (23.69) and the largest area-weighted mean patch size (6381.8 ha).

Discussion

The results of our analysis show that the extent of MPB-impacted lodgepole stands (using the 31–100% mortality bins) was approximately half the area of regenerating conifer in 1915 that converted to mature conifer following the fires of 1889 and 1905 (Figs. 3 and 5). It is likely, then, that

Table 3 Change matrix for landcover classes from 1915 (left) to 2020/22 (top)

Landcover class	Mature conifer	Broadleaf/ mixed wood	Regenerating conifer	Shrub	Herbaceous	Wetland	Water	Barren ground
Mature conifer	4823.8	49.6	3.3	105.2	89.8	73.1	68.3	114.1
Broadleaf/mixed wood	80.0	29.0		4.9	3.3	0.3	0.1	1.7
Regenerating conifer	13,740.6	473.2	1.2	111.4	175.7	75.6	35.8	208.9
Recently burned	101.5					0.0	0.0	0.0
Shrub	2011.6	85.7	40.7	273.7	71.2	72.0	57.3	137.7
Herbaceous	219.5	6.1	0.2	40.9	273.0	0.0	0.2	38.9
Wetland	112.2	3.7		42.4	1.5	264.9	50.6	4.3
Water	184.7	2.5		48.1	4.7	43.3	941.0	56.8
Barren ground	508.6	8.8	8.4	66.0	21.3	7.9	53.2	290.2

Fig. 5 Map showing area of 1915 landcover classes that transitioned to mature conifer in 2020/22. Blank areas on the map did not transition to another class

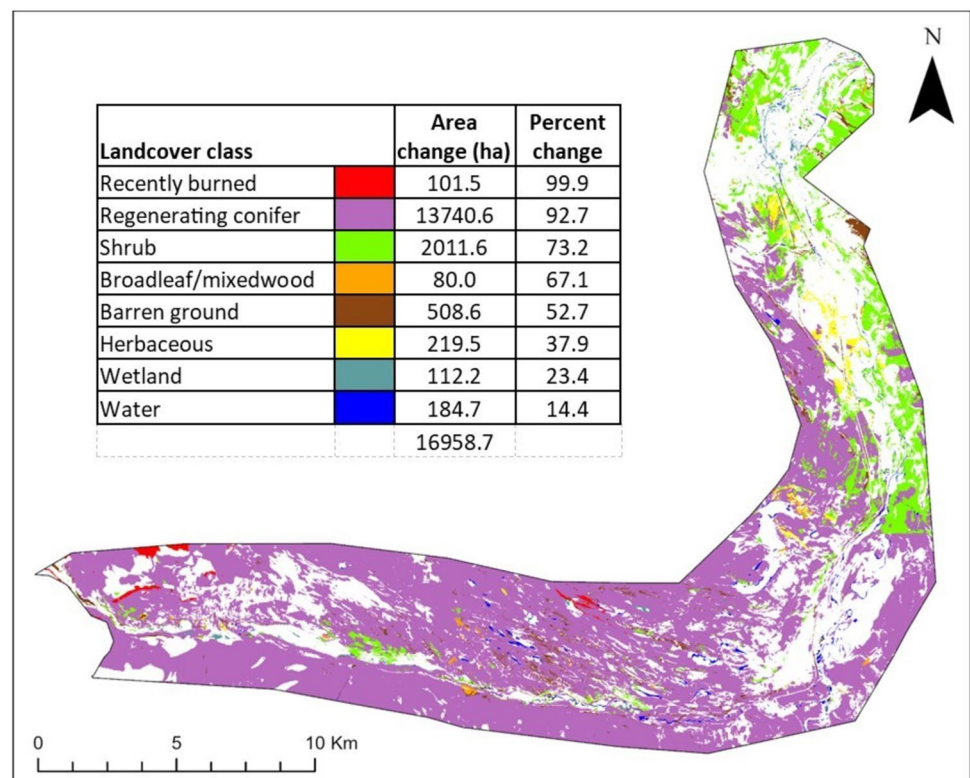


Table 4 Area (ha) and percent of classes in the 1915 landcover map that would be impacted by MPB (using all mortality bins) a century later

MPB severity	Mature conifer	Broadleaf/mixed wood	Regenerating conifer	Recently burned	Shrub	Herbaceous	Wetland	Water	Barren ground	Grand Total
1–10%	163.2	0.1	593.7	7.7	26.1	1.1		0.1	9.1	801.1
11–20%	256.7	3.5	1042	7.6	113.9	5.5	0.4	2.8	38.7	1471.1
21–30%	229.5	4.8	1301.3	13.1	102.5	20	1.3	0.8	50.1	1723.3
31–40%	212.8	6.9	1207.4	8.9	131.2	12.6	0.5	0.3	35.7	1616.4
41–50%	159.3	10.6	1479.9	18.4	93	3.3	0.5	1.7	37.3	1804
51–60%	217.6	6.1	1225.8	11.6	51.2	27	0.3	0.6	29.9	1570.3
61–70%	168.8	0.2	839.5	0.6	24.4	0.5	0.4	0.8	19.4	1054.5
71–80%	127.5	2.6	648	1.6	16.7	17.3	0.3	0.8	23.8	838.6
81–90%	68.6	5.2	325.7	0.7	30.3	33.3	0	0.3	4.6	468.5
91–100%	146.8	0.1	273.3	0.1	101.8	11.9	2	2.4	22.1	560.5
Total area	1751	40.1	8936.5	70.2	691.1	132.4	5.6	10.6	270.7	11908.4
Percent area	32.90%	33.70%	60.30%	69.20%	25.10%	22.90%	1.20%	0.80%	28.10%	45.10%

the MPB will have significant influence on future ecosystem composition in the study area. The outbreak has also reduced the area-weighted mean patch size for mature conifer from 15,228 ha in 2020/22 landcover map to 6381.8 ha in the MPB-adjusted 2020/22 landcover map. Further, the area-weighted mean shape index of 23.69 for mature conifer in the MPB-adjusted 2020/22 map is similar to the area-weighted mean shape index of 25.91 for regenerating conifer in the 1915 landcover map. The novel MPB disturbance has therefore returned some heterogeneity to the landscape by reducing the area-weighted mean patch size of the mature conifer and reintroducing a comparable amount of spatial complexity to the dominant landcover class (Table 2, Fig. 4).

The legacy of the frequent, mixed-severity fire regime in Jasper NP is evident on the 1915 landcover map, with over half over the study area comprising regenerating conifer (56.4%). Prior to the policy of fire suppression established circa 1913, large stand-replacing fires occurred on average every 65 years since the Little Ice Age in the study area (Chavardès and Daniels 2016; Tande 1979). The most recent of these large fires occurred in 1889 and 1905, resulting in older cohorts of regenerating conifer (i.e., 26 years old) visible in the 1915 imagery adjacent to the Miette River from the town center to the western park entrance, and younger cohorts (i.e., 10 years old) east of the town and west of the Athabasca River (Chavardès and Daniels 2016; Tande 1979). Large areas of shrub (10.4%) on the eastern side of the Athabasca River and north of its confluence with the Snaring River contribute to the open, patchy configuration of the landscape in 1915. Stands of mature conifer, with an area-weighted mean patch size of 226.5 ha, comprise 20.1% of the study area.

Continuous coniferous species cover dominates the study area in the 2020/22 landcover map (82.7%), with fewer and larger patches as a consequence of the altered fire regime since

1913. In the absence of frequent fire, 92.7% of regenerating conifer in the 1915 landcover map (i.e., over half the study area) succeeded to mature conifer forest. Similarly, a large percentage of shrub (73.2%) also transitioned to the mature conifer class. Smaller areas of transition to mature conifer occurred across all the other classes. However, some of these changes are a result of obscuring issues associated with georeferencing oblique images, especially for the barren ground and water classes, which affected the accuracy of the 2020/22 landcover map. For example, although portions of barren ground, which includes exposed soil, would have likely transitioned to mature conifer, other areas that include rock that were previously visible in the historical photographs are now obscured by mature conifer. This issue occurs frequently north of the Miette River and includes areas where the full extent of lakes have also become obscured by mature conifer.

The spatial extent of the 1889 and 1905 fires is evident in the pattern of regenerating conifer in the 1915 landcover map (Fig. 4). Our results show where regenerating conifer (and other landcover classes) in the 1915 landcover map successfully transitioned to mature conifer forest in the 2020/22 landcover map (Fig. 5). Given the dates of the two stand-replacing fires, the age class for this mature forest would have been between 105 and 121 years old when the MPB outbreak started in the park circa 2010. Stands of this age class are considered highly susceptible to MPB in epidemic phase (Saf-ranyik and Carroll 2006; Taylor and Carroll 2004).

Within the study area, we estimate that 11,484 hectares of mature conifer were impacted by MPB. This value is smaller than the total area reported by the VRI data because it only accounts for the areas of mature conifer overlapping in the 2020/22 landcover map. This discrepancy relates to some of the VRI polygons comprising multiple tree species (i.e., lodgepole pine may be the dominant species within the

polygon, but other species such as white spruce or Douglas fir may also be present). Stands with a high percent of mortality (i.e., > 70%) occur throughout the study area (see Fig. 3), specifically south and east of the townsite, the middle portion along both sides of the Miette River, north of the Miette near the western entrance, and the upper elevations toward the northern extent. In stands of high mortality, field surveys undertaken by the University of Lethbridge between 2021 and 2023 indicate a lack of conifer seedling regeneration (Tristan Skretting, personal communication, 26 April 2024). These findings are consistent with previous studies investigating seedling recruitment in lodgepole forests with high MPB mortality in central BC and western Alberta (Astrup et al. 2008; Lieffers et al. 2023; McIntosh and Macdonald 2013).

Time will tell how the forests in Jasper NP will recover from this recent novel disturbance and what the future species composition will look like. A key difference between the processes of MPB and fire is that the latter only disturbs pine species (Meyer et al. 2021). However, a study by Dordel et al. (2008) in Banff and Kootenay National Parks suggests that MPB infestations can have similar effects on stand structure to those of fire, and lead to more open and diverse forests (also see McCullough et al. 1998). In Jasper NP, lodgepole pine stands with low MPB mortality could slowly diversify as canopy openings result in releases of more shade-tolerant species such as Douglas fir and white spruce from the understory (Canham 1989). Stands with higher mortality could see further diversification due to the limited seedling recruitment of lodgepole pine or conversion to herbaceous ecotypes (Lieffers et al. 2023). Monitoring programs can track these changes and be used to inform management.

New compounding disturbances will also influence the recovery and future composition of species in the study area. The timing and intensity of these disturbances can affect the material legacies required for recovery after the initial disturbance (Paine et al. 1998). Since this analysis was completed, the 33,108 ha Jasper Wildfire Complex burned through the upper Athabasca River valley in late July 2024, including 3392 ha (12.84%) of the study area. Approximately 70% of the total area burned by the Jasper Wildfire Complex was in forest stands affected by MPB (Government of British Columbia 2022; Jasper National Park 2024). Although the fire tragically destroyed up to 30% of physical infrastructure in the town of Jasper, it may benefit the recovery of lodgepole stands impacted by MPB. Lodgepole pine are a fire-adapted species and are reliant on fire to release cohorts of unopened cones on their branches and expose viable seedbeds by removing prohibitive understory, forest litter, and feathermosses (Astrup et al. 2008; Lieffers et al. 2023).

However, without fire, lodgepole pine seeds typically become unviable 20 years after the trees die. This scenario could increase the likelihood of species shifts in stands with higher MPB mortality. In contrast, fir and spruce species can

only produce viable seedlings from living trees. Hence, a high severity fire that occurs in high mortality MPB stands after lodgepole seedlings become unviable, and kills fir and spruce species, could initiate a transition to non-forest in some areas (i.e., Parks et al. 2019).

Conclusion

Disturbance is a vital attribute of spatial and temporal variability in most ecosystems (Landres et al. 1999). The dominant disturbance in the study area since the Little Ice Age has been fire, which has strongly influenced the HRV of the montane ecoregion in the park. The landscape adapted to this disturbance, and Fig. 4 demonstrates the successful regeneration of coniferous species following the large 1889 and 1905 fires. The implementation of fire suppression policies over the previous century resulted in ecosystems departing from their HRV as fire frequency decreased considerably, leading to increased homogeneity on the landscape characterized by mature, closed canopy coniferous forests (Rhemtulla et al. 2002). This departure from HRV, because of the altered fire regime, has directly contributed to the considerable extent of the novel insect disturbance. With an intact fire regime, reflecting landcover composition and patterning evident in 1915, the extent of the MPB in the study area would likely be significantly different.

This study indicates that the novel insect disturbance in Jasper NP can restore landcover composition and pattern lost to fire suppression in the montane ecoregion. However, successional responses in stands with high MPB mortality and the timing of future disturbance could lead to species shifts or transitions to non-forest. Coupled with climate change-driven conditions, these potential transitions could increase the departure from the HRV and shift the composition, function, and pattern of landscapes under Parks Canada's management. It seems plausible, perhaps likely, that montane ecosystem in Jasper will undergo significant transitions that will necessarily involve shifts in how they are managed. Increased novelty suggests managing with history in mind but not necessarily as a specific target (Higgs et al. 2014).

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10113-024-02356-8>.

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Data Availability Data is available upon request.

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