

Literature Review

Caribou, Fire, and Forestry

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1. BACKGROUND

Woodland caribou (*Rangifer tarandus*) (hereafter 'caribou') are declining across Canada and are listed as threatened under the Canadian Species at Risk Act. Anthropogenic disturbance, primarily resource extraction by the forestry and oil and gas sectors, is the ultimate cause of caribou declines (Vors & Boyce 2009; Environment Canada 2012). Anthropogenic disturbance removes and fragments caribou habitat, creates early seral habitat favourable to apparent competitors of caribou – moose (*Alces alces*), deer (*Odocoileus* spp.), and elk (*Cervus canadensis*), and creates movement routes for predators of caribou (DeCesare *et al.* 2010; Serrouya *et al.* 2017; Mumma *et al.* 2018). Combined, the impacts of anthropogenic disturbance have a negative influence on caribou survival and population recruitment by increasing the density and distribution of apparent competitors and predators, and increasing caribou predation rates (Sorensen *et al.* 2008; Environment Canada 2012; Hervieux *et al.* 2013; Serrouya *et al.* 2021). Mitigating the negative impacts of anthropogenic disturbance on caribou through habitat restoration and landscape management are immediate priorities of federal and provincial caribou recovery efforts (Environment Canada 2012; Government of Alberta 2017).

Wildfire is the dominant stand-replacing disturbance across the boreal forest, and in recent decades there has been increasing focus on sustainable forest management practices that mirror natural disturbances like fire (Bergeron *et al.* 2001; Harvey *et al.* 2002). Landscape management that emulates natural disturbance regimes from coarse- to fine-scales (wildfire size, severity, and frequency) is more likely to maintain boreal forest biological diversity and ecosystem function (Franklin 1993; Gauthier, Leduc & Bergeron 1996; Angelstam 1998; Bergeron & Flannigan 2004; Bichet *et al.* 2016), and could benefit caribou (Rempel & Kaufmann 2003; Dhital *et al.* 2013; Donovan, Brown & Mallory 2017). In Alberta, future forest harvesting in caribou ranges will be required to emulate natural disturbances via aggregate harvesting; creating large areas of early seral habitat and large patches of intact forest (Government of Alberta 2017). At the stand-scale, silvicultural practices that mirror the natural variability of stand structure and understory succession across burned areas may reduce the current disjunction between understory succession in, and wildlife use of, burned versus harvested areas (Bergeron & Flannigan 2004). This disjunction includes differences in the responses of caribou, their alternate competitors, and predators to burned versus harvested areas, irrespective of stand age (e.g., Rempel *et al.* 1997; Environment Canada 2012; Fryxell *et al.* 2020).

With of goal of understanding how silviculture and harvesting practices might mirror those of natural disturbances, here we summarize research describing differences in responses of caribou and caribou forage (i.e., terrestrial and



arboreal lichens) to forestry and wildfires. We recognize that achieving self-sustaining caribou herds will require coarse and fine-scale management strategies that evaluate the potential impacts of these disturbances beyond caribou habitat use and forage. However, addressing the direct impacts of forestry versus wildfires on primary prey, predators, and their food was outside the scope of this literature review.

2. HABITAT SELECTION AND DISTRIBUTION

2.1. WILDFIRE

To varying degrees, early-seral stage forests created by wildfires are avoided by caribou (Joly *et al.* 2003; Dalerum, Boutin & Dunford 2007; Shepherd, Schmiegelow & Macdonald 2007; Robinson *et al.* 2012; Johnson, Ehlers & Seip 2015; Konkolics 2019; Lafontaine *et al.* 2019; Silva *et al.* 2020). Caribou generally do not alter their home range in response to wildfires (Dalerum *et al.* 2007; Faille *et al.* 2010), but instead avoid the burned portions of the home range (Schaefer & Pruitt 1991; Joly *et al.* 2003), although variation among individuals and landscapes has been reported. For example, caribou in wildfire-dominated landscapes may shift home ranges to include more burned habitat (Silva *et al.* 2020), and caribou avoidance of burned habitat may decrease in areas with high densities of wildfires (Lafontaine *et al.* 2019). Caribou response to burned habitat is also influenced by their historical exposure to wildfires; boreal caribou populations in Quebec with frequent exposure to wildfire avoided recent burns and harvested areas (< 5 years), while populations without previous exposure to wildfire selected for those disturbances (Lafontaine *et al.* 2019). In Jasper National Park, caribou select old forest (> 75 years) in areas that experienced less frequent wildfires (Shepherd *et al.* 2007).

Caribou avoidance of burned areas is likely primarily driven by reduced lichen forage availability and the increased predation risk associated with those habitats (Bergerud 1974; Schaefer & Pruitt 1991; Fisher & Wilkinson 2005; Dunford *et al.* 2006; Shepherd 2006; Courtois *et al.* 2007; Joly, Chapin & Klein 2010; Robinson *et al.* 2012), although the relative influence of forage availability versus use by primary prey and associated predation risk varies across different landscapes (DeMars *et al.* 2019) and with reproductive status (Leblond *et al.* 2016; Viejou *et al.* 2018). Specifically, caribou generally avoid burned habitat between 6 and 60 years post-fire (Klein 1982; Schaefer & Pruitt 1991; Joly *et al.* 2003; Fisher & Wilkinson 2005; Dalerum *et al.* 2007; Lafontaine *et al.* 2019), and even when terrestrial lichen forage is available (Thomas, Barry & Alaie 1996a). During the calving season, when caribou prioritize minimizing predation risk over access to forage (Leblond *et al.* 2016; Skatter *et al.* 2017; Viejou *et al.* 2018), boreal caribou in northern Saskatchewan select recently burned (< 5 years) habitat and remnant habitat within recent burns in areas



where anthropogenic disturbance is low (Skatter *et al.* 2017; Silva *et al.* 2020). However, caribou in north-eastern British Columbia select burned habitat during all seasons (Mumma *et al.* 2018), while caribou in northern Alberta avoid burned habitat and residuals in all seasons (Konkolics 2019). In the southern Yukon, caribou generally avoided burns and areas close to burns, but the strength of that relationship varied among individual animals (Russell 2018). Areas within the core of wildfires < 50 years old are avoided more than areas within 500m of the edge of wildfires (Joly *et al.* 2003), although remnant forest within burned areas may be selected in some areas (Skatter *et al.* 2017; Russell 2018).

The seasonal selection of recently burned habitat in some areas may be due to the decrease in understory vegetation and forage quality immediately post-fire, which may decrease predation risk by reducing the presence of primary prey and increasing the ability of caribou to detect predators (Ballard *et al.* 2000; Street *et al.* 2015; Skatter *et al.* 2017). Also, caribou may select for emerging green vegetation in new burns during spring or summer. Remnant unburned patches within a burn perimeter, may provide foraging habitat for caribou during winter (Russell 2018).

The combined impacts of climate change, mountain pine beetle infestations, and historical forest management are likely to change the size, frequency, and severity of wildfires in the future (Wang *et al.* 2014; Hanes *et al.* 2018; Bleiker *et al.* 2014). These changes have the potential to alter caribou habitat selection and distribution, decrease caribou forage, and increase early seral vegetation, causing increased predation risk (Palm *et al.* in review; Rupp *et al.* 2006; Barber *et al.* 2018) (see 'Forage' and 'Mortality').

2.2. FORESTRY

Across much of the boreal forest, caribou prefer the mature forest stands that are also valuable to the forest sector (Stevenson & Hatler 1985; Hervieux *et al.* 1996; Courbin *et al.* 2014). However, in some areas and seasons caribou select stands with low timber volumes, a high percentage of non-merchantable trees, or forest types which are of less value for harvesting (e.g., peatlands; Terry, McLellan & Watts 2000; Latham *et al.* 2011; DeMars & Boutin 2018).

Harvest blocks are generally avoided by caribou regardless of ungulate forage availability (Smith *et al.* 2000; DeCesare *et al.* 2012; Peters *et al.* 2013; Gagné, Mainguy & Fortin 2016; Leblond *et al.* 2016; Mumma *et al.* 2018). Harvesting can shift or change the size of home ranges (Smith *et al.* 2000; Vors *et al.* 2007; Faille *et al.* 2010; Honsberger 2011; Slater 2013; Beauchesne, Jaeger & St-Laurent 2014; MacNearney *et al.* 2016; Donovan *et al.* 2017), and change how caribou move within their home ranges (Chubbs *et al.* 1993; Cumming & Beange 1993; Smith *et al.* 2000; Rettie & Messier 2000; Schaefer, Bergman & Luttich 2000; Mahoney & Virgl 2003; Vors *et al.* 2007; Faille *et al.* 2010; Honsberger 2011; Slater 2013; Beauchesne *et al.* 2014; MacNearney *et al.* 2016; Donovan *et al.* 2017). In addition, the location of harvesting relative to home ranges, and the configuration of forest patches and harvesting within home ranges, can



impact how caribou respond to harvesting. For example, in Ontario, caribou were closer to clear cuts as harvesting increased *around* their home range, and were farther from clear cuts as harvesting increased *within* their home range (Donovan *et al.* 2017). In Quebec, caribou selected young clear cuts (6-20 years old) that were adjacent to mature (90-120 year old) forest stands (Hins *et al.* 2009). In the short-term, human activity associated with harvesting elicits a short-term avoidance response from caribou (Cumming & Hyer 1998; Smith *et al.* 2000), while in the long-term clear cuts < 40 years old are generally avoided at broad scales (Cumming & Beange 1993; Rettie & Messier 2000; Courtois *et al.* 2007; Vors *et al.* 2007; DeCesare *et al.* 2012; Rudolph, MacNearney & Finnegan 2019). Avoidance of clear cuts is more prevalent in female caribou than males (Schaefer & Mahoney 2007) and can vary with reproductive status (Leblond *et al.* 2016). In Quebec, female caribou with calves selected harvest blocks < 20 years old, potentially prioritizing reducing predation risk from wolves over access to forage and reducing predation risk from bears (Leblond *et al.* 2016).

Within managed forests, caribou select mature forest and protected blocks (Chubbs *et al.* 1993; Courtois *et al.* 2008; Courbin *et al.* 2009; Bowman *et al.* 2010; Gagné *et al.* 2016). Connectivity between protected blocks is important (Seip 2008; Courbin *et al.* 2014; O'Brien *et al.* 2016), but movement or migration between protected blocks may expose caribou to predation risk (Seip 2008; Blagdon & Johnson 2021). Likewise, in harvested areas, smaller protected blocks and blocks adjacent to recently harvested stands may be ecological traps for caribou, exposing them to the increased predation risk associated with early seral stands (Courbin *et al.* 2009, 2014).

Clear cut harvesting can also influence the selection of habitat by caribou. Females displaced by clear cutting within their home ranges selected mature black spruce forests, while females who were not displaced continued to use all habitat types in proportion to their availability (Chubbs *et al.* 1993). During calving and summer, caribou in harvested landscapes select closed canopy mature conifer forest, while caribou in unharvested landscapes show an equal preference to mixed/deciduous stands, open canopy mature conifer stands, and closed canopy mature conifer stands (Moreau *et al.* 2012).

In comparison to clear cut harvesting, partial cut harvesting is expected to have less impact on caribou habitat use (Stevenson *et al.* 2001), although there is only limited evidence of caribou using partial cuts more than clear cuts (Serrouya *et al.* 2006), and caribou may select salvage logged landscapes even less than clear cuts (Seip & Jones 2008). Retention patches (at a minimum of 20% of initial block) are positively correlated with caribou use of clear cuts 15-18 years post-harvest (Franklin, Macdonald & Nielsen 2019). In Quebec, habitat conditions in stands that were harvested with retention of merchantable stems, retention of seed-trees, and using partial cut harvesting, are different from those of mature forest stands (Nadeau Fortin, Sirois & St-Laurent 2016). Initial results from a study in BC suggest that



group selection harvesting (< 1 ha cut) was useful for retaining arboreal lichen, but can create habitat that favours the apparent competitors of caribou (moose and mule deer) and their shared predators (bears and wolves; C. Johnson Unpub. Data).

3. MOVEMENT

3.1. WILDFIRE

By 5 to 10 years post-fire, burned habitats have higher densities of downed trees and understory vegetation compared to unburned habitats (Schaefer & Pruitt 1991; Metsaranta, Mallory & Cross 2003), which can restrict caribou movement (Schaefer & Pruitt 1991; Metsaranta *et al.* 2003; Shepherd *et al.* 2007). However, research within the range of the Beverly barren ground caribou population (DU 3; COSEWIC 2011) found no evidence of restricted movements through any age of burn surveyed (1-250 years) (Thomas *et al.* 1996a). Because post-fire coniferous forests have lower canopy density, wildfires can influence the accumulation and melting rates of snow when compared to unburned stands (Kirchhoff & Schoen 1987; Skidmore 1994; Winkler 2011; Maxwell, Call & St. Clair 2019). Caribou are adapted for movement through snow, but deep snow can restrict movement and increase energy expenditure (Telfer & Kelsall 1984; Fancy & White 1985; Stuart-Smith *et al.* 1997; Avgar *et al.* 2013). Deep and hard snow depth reduces and increased access to terrestrial and arboreal lichens respectively (see 'Forage'), which in turn alters habitat use at fine scales (Schaefer & Pruitt 1991; Johnson, Parker & Heard 2001; Szkorupa 2002). Snow depth and hardness also influence movements of primary prey and predators, notably at shallower snow depths than they influence those of caribou (Telfer & Kelsall 1979, 1984; Droghini & Boutin 2018).

3.2. FORESTRY

Harvesting in caribou ranges disrupts normal caribou movement patterns (Bloomfield 1979). Daily movement rates decline with increasing harvest within home ranges (Smith *et al.* 2000), and the response can vary between sexes, with females moving 2-3 times further from harvesting than males (Chubbs *et al.* 1993). Early-seral forest created by clear cut harvesting is a recognized barrier to caribou movement (Stevenson *et al.* 2001; Apps & McLellan 2006), as are roads built for forest harvesting (Dyer *et al.* 2002). Harvesting reduces canopy cover (Telfer 1978), and reduced canopy cover is associated with increased snow depth and hardness (Kirchhoff & Schoen 1987), but see (Jones 2007). Changes in snow depth and hardness can impact caribou movements and foraging (see 'Movement – Wildfire').



4. DEMOGRAPHY

4.1. MORTALITY

4.1.1. Wildfire

Neither the presence of burned areas nor amount of home range burned predicts mortality rates of female caribou (Dalerum *et al.* 2007; Konkolics 2019; Johnson *et al.* 2020; Stewart *et al.* 2020). At fine scales, use of recently burned habitats and habitat modifications caused by wildfires, including greater edge habitat and younger stand age, do not increase mortality risk of caribou (Apps *et al.* 2013; Konkolics 2019), but do increase caribou-predator overlap (Robinson *et al.* 2012). However, caribou habitat use prior to being killed by predators also influences predation risk (Leblond, Dussault & Oullett 2013; McKay *et al.* 2021), and it is likely that the contribution of burned habitat to caribou mortality risk may apply at coarser spatial and temporal scales than have been evaluated to date. Primary prey respond positively to early seral habitat created by wildfires (Boyce *et al.* 2003; Maier *et al.* 2005; Lord & Kielland 2015; Joly *et al.* 2016), although this varies with wildfire age, severity, and area (Maier *et al.* 2005; Brown *et al.* 2017; Roerick, Cain III & Gedir 2019; DeMars *et al.* 2019). In turn, increases in primary prey are linked to the distribution and densities of their predators (Hebblewhite, Munro & Merrill 2009; Serrouya *et al.* 2017; Kittle *et al.* 2017), and increases predation risk for caribou areas where they co-occur with primary prey (Peters *et al.* 2013; Mumma *et al.* 2018). Although studies to date have not detected direct links between caribou mortalities and wildfires, it is likely that the impact of wildfires on caribou are synergistic with those of other disturbances which create early seral stage habitat and predator travel routes within caribou ranges.

4.1.2. Forestry

The area of anthropogenic disturbance (including harvesting) influences the mortality rate of female caribou (Grant, Johnson & Thiessen 2019; Johnson *et al.* 2020). Predation is more likely to occur on harvested landscapes than unharvested landscapes (Fryxell *et al.* 2020), and in home ranges with low proportions of old forests (> 140 years) (Wittmer *et al.* 2007). Female caribou are more likely to be killed than males as the amount of disturbance in their home range increases (Courtois *et al.* 2007). At fine-scales, caribou mortality risk is not associated with areas with higher proportions of younger forests or edge habitat (Apps *et al.* 2013), but this is likely because caribou already avoid harvested areas at coarse spatial scales (DeCesare *et al.* 2012). Roads created to access harvest blocks directly increase caribou predation risk (DeCesare *et al.* 2014), as they are used by predators for travel (James & Stuart-Smith 2000; Dickie *et al.* 2017; Mumma *et al.* 2018; Blagdon & Johnson 2021), and result in increased caribou-wolf encounters (Whittington *et al.* 2011; Mumma *et al.* 2017). The early seral habitat produced by harvesting has a negative influence



on caribou survival by increasing the density and distribution of primary prey and their predators (Leblond *et al.* 2016; Serrouya *et al.* 2017; Anderson, McLellan & Serrouya 2018), and increasing caribou predation rates (Cumming & Beange 1993; Courbin *et al.* 2014; Leblond *et al.* 2016; Serrouya *et al.* 2021). Primary prey may also prefer partial cuts to clear cuts (Eastman 1974; C. Johnson Unpub Data).

4.2. RECRUITMENT AND POPULATION GROWTH

4.2.1. Wildfire

Wildfire accounts for 5% of the variation in boreal caribou calf recruitment rates across Canada, although the contribution of wildfires and other disturbances to recruitment and population growth are cumulative (Sorensen *et al.* 2008; Environment Canada 2011). Wildfire may not negatively impact recruitment in the short term (e.g., 5 years following wildfire; Dalerum *et al.* 2007), but models show that as proportion of area burned increases, caribou calf:cow ratios decrease (Johnson *et al.* 2020). However, recruitment rates of caribou may be more resilient to high annual burn rates in the absence of additional anthropogenic disturbance (Stewart *et al.* 2020).

4.2.2. Forestry

Anthropogenic disturbance, including harvest blocks, accounts for 65% of the variation in boreal caribou recruitment across Canada (Environment Canada 2011). As the proportion of early and mid-seral stage forest increases within caribou home ranges, caribou survival decreases (Wittmer *et al.* 2007; Grant *et al.* 2019; Fryxell *et al.* 2020). In some areas, broad-scale forest harvesting has resulted in the extirpation of caribou from low-elevation valley bottoms (Poole, Heard & Mowat 2000). However, in the short-term (< 5 years after harvest), caribou herds may remain stable despite an increase in total area harvested from ~45% to over 60% (Mahoney & Virgl 2003). Also, one might expect a lag of up to 20 years between forest harvesting and caribou decline and extirpation (Vors *et al.* 2007). Caribou population declines are strongly correlated with a reduction in high-quality habitat resulting from forest harvesting (and oil and gas activities) (Johnson *et al.* 2015).

5. FORAGE

5.1. WILDFIRE

Terrestrial and arboreal lichens are the dominant food source for caribou during winter, and are also consumed during summer (Klein 1982; Edmonds & Bloomfield 1984; Schaefer & Pruitt 1991; Thomas, Edmonds & Brown 1996b; Johnson *et al.* 2001; Bergerud, Luttich & Camps 2008; Thompson *et al.* 2015; Denryter *et al.* 2017). Large wildfires typical of the



boreal ecosystem initially reduce/remove available terrestrial lichen; pioneer species like bryophytes and vascular plants dominate burned habitat for the first 25-40 years until terrestrial lichens recover (Russell & Johnson 2019). In more productive stands, feathermosses can replace lichens 70-300 years post-disturbance (Stevenson *et al.* 1991; Coxson & Marsh 2001; Joly *et al.* 2003; Dunford *et al.* 2006; Hart & Chen 2006, 2008; Dalerum *et al.* 2007; Collins *et al.* 2011; Mallon *et al.* 2016). Arboreal lichens are present approximately 60 years after stand-replacing wildfires, but are most abundant in stands > 100 years old (Foster 1985; Berryman & McCune 2006; Horstkotte *et al.* 2011).

Successional stages and timing of succession vary with local conditions like soil moisture, acidity, and topography, as well as between pine-lichen and spruce-lichen sites (Kershaw 1977; Foster 1985; Brullsaer, Bradfield & Maze 1996; Arseneault, Villeneuve & Boismenu 1997; Coxson & Marsh 2001; Hart & Chen 2006; Bergeron & Fenton 2012; Russell & Johnson 2019). For example, in peatlands in Alberta, terrestrial lichen regrowth is slow for the first 20 years following wildfire, peaks at 46 years after fire, and decreases in stands > 70 years after fire (Dunford *et al.* 2006). In the north of Quebec, bryophytes and vascular plants dominate burned habitat < 30 years after fire, after which lichens dominate (Arseneault *et al.* 1997). In the central-interior of British Columbia, bryophytes and *Stereocaulon* spp. dominate stands < 20 years following wildfire, *Cladonia* spp. dominate between 20 and 50 years after fire, *Cladonia* spp. and *Cladina* spp. dominate between 50 and 150 years after fire, and feathermosses overgrow the terrestrial lichen mat in stands 100-150 years after fire (Brullsaer *et al.* 1996; Coxson & Marsh 2001; Sulyma & Coxson 2001). In contrast, in the pine and pine/spruce stands in the Tweedsmuir area of west-central British Columbia, the understory does not shift from terrestrial lichens to feathermosses until 200-300 years following wildfire (Cichowski & Banner 1993). Across caribou ranges, where xeric acidic soils limit growth of vascular plants and bryophytes, terrestrial lichens may be the dominant ground cover in stands as young as 10 years after burning and can persist beyond 300 years (Kershaw 1977; Brullsaer *et al.* 1996). In comparison to stand-replacing wildfires, terrestrial and arboreal lichens can be resilient to low-intensity wildfires (Miller, Root & Safford 2018), although burning can decrease the diversity and abundance of arboreal lichens close to the ground (Ray, Barton & Lendemer 2015).

Bryophytes and vascular plants available after wildfire can supplement caribou diet (Thomas *et al.* 1996b; Rettie, Sheard & Messier 1997; Denryter *et al.* 2017); however, the temporal availability of the post-fire vegetation is limited and can be of low nutritional value to caribou (Joly *et al.* 2003; Denryter *et al.* 2017). While terrestrial lichen production slows in older stands, it is debated whether burning forests to encourage an increase in terrestrial lichen growth would be beneficial to caribou populations (Klein 1982; Shepherd 2006), as multiple studies found caribou select forests > 100 years old (Thomas *et al.* 1996a; Apps *et al.* 2001; Szkorupa & Schmiegelow 2003). Also, arboreal lichens, typically a secondary forage in low-elevation forests, are largely absent from stands < 60 years old (Foster 1985; Berryman &



McCune 2006; Shepherd 2006; Horstkotte *et al.* 2011). In addition, early seral vegetation created by burns will increase the apparent competitors of caribou, primarily moose and deer, as well as their shared predators. Unsustainable predation is the primary limiting factor for most populations of caribou, thus, fire or forestry related increases in the distribution or abundance of predators result in a net negative outcome for caribou even if there was a concurrent gain in the productivity or availability of lichen (see 'Mortality').

As previously stated, wildfires can influence overall snow accumulation and ablation rates (Maxwell *et al.* 2019). Increased snow depth and snow hardness can limit access to terrestrial lichens, and can shift caribou foraging from terrestrial lichens to arboreal lichens (Thomas *et al.* 1996b; Johnson *et al.* 2001, 2004; Kinley *et al.* 2007); in areas with a consistent deep snowpack, southern mountain caribou (DU9; COSEWIC 2011) feed almost exclusively on arboreal lichens during winter (Terry *et al.* 2000). With climate change, the confounding impacts of wildfires and changes in precipitation and temperate (e.g. rain-on-snow events; Putkonen & Roe 2003) may increase the importance of arboreal lichens in boreal, northern, and central mountain caribou diets.

5.2. FORESTRY

Forest harvesting generally reduces the abundance of terrestrial lichens, with lichen abundance decreasing approximately 2 years after harvesting (Coxson & Marsh 2001; Waterhouse, Armleder & Nemec 2011). Winter harvesting (in the absence of mechanical site preparation) results in less damage to understory vegetation and terrestrial lichens when compared to both summer harvesting and burning (Kranrod 1996; Webb 1998; Coxson & Marsh 2001; Hart & Chen 2008; Lafleur *et al.* 2016; Nobert *et al.* 2020). When ground disturbance during harvesting is low, the understory communities in harvested stands may initially be similar to pre-harvest conditions, until the absence of canopy cover and associated changes in light, temperature and humidity result in changes in the understory community (Nguyen-Xuan *et al.* 2000; Hart & Chen 2006, 2008). Generally, vascular plants (including forbs, graminoids, and shrubs) dominate the understory 7-25 years post-harvest. In stands > 25 years post-harvest terrestrial lichen biomass increases in stands. Within 20-30 years, understory communities of harvested-origin stands begin to converge with those of fire-origin stands of a similar age, and harvested stands and fire-origin stands become largely similar to one another 100 years post-disturbance (Bergeron & Dubue 1988; Nielsen *et al.* 2004; Hart & Chen 2008). However, like burned stands, successional pathways differ across ecosite types and local conditions. For example, in spruce-lichen forests in Quebec, terrestrial lichen biomass was similar between fire- and harvest-origin stands as soon as 4-13 years post-disturbance (Lafleur *et al.* 2016). In jack pine and black spruce stands in northern Ontario, terrestrial lichens were largely absent (< 10% cover) from burned stands 3-16 years post-disturbance, but were present in harvested stands irrespective of age (~30%) (Webb 1998).



Harvesting both directly reduces the available arboreal lichen by removing trees and snags, and indirectly reduces lichens by increasing wind exposure on the residual trees (Stevenson *et al.* 2001). Arboreal lichens are largely absent from stands until they are 60 to 100 years old (Foster 1985; Berryman & McCune 2006; Horstkotte *et al.* 2011).

Different harvesting and silvicultural practices (timing, site preparation, density of stems removed) have differing impacts on the regrowth of lichens and vascular plants (Kranrod 1996; Stevenson *et al.* 2001; Coxson, Stevenson & Campbell 2003; Triton 2005; Waterhouse, Armleder & Linnell Nemec 2007; Waterhouse *et al.* 2011; Nadeau Fortin *et al.* 2016; Vitt, Finnegan & House 2019). Winter harvest on snow results in less disturbance of terrestrial lichens when compared to summer harvest (Kranrod 1996; Coxson & Marsh 2001). Scarification causes a decrease in terrestrial lichens (Kranrod 1996), but has variable impacts on vascular plants, with some plants responding positively to the scarification process (e.g., *Equisetum* spp., *Vaccinium vitis-idaea*) while others are negatively associated with scarification (e.g., *Shepherdia canadensis*, *Hedysarum* spp.) (Nielsen *et al.* 2004). Stump-side de-limbing has less impact on the abundance of terrestrial lichens than road-side de-limbing (Kranrod 1996). Herbicide application post-harvest inhibits growth of conifer competitors like shrubs and grasses (McCormack 1994), but can also decrease terrestrial lichen abundance and species richness (Newmaster, Bell & Vitt 1999).

Partial-cut harvesting (either group selection or single tree selection) may mitigate some of the impacts of harvesting relative to the availability of terrestrial and arboreal lichens as well as early seral vegetation (Vitt & Mooneyhan 2005; Nadeau Fortin *et al.* 2016; Vitt *et al.* 2019). Group or single tree selection maintains arboreal lichen in the residual trees immediately post-harvest (Coxson *et al.* 2003), although arboreal lichen in partial cut stands are at increased risk of wind exposure (Stevenson *et al.* 2001). Single-tree harvest does not decrease the biomass of arboreal lichen per tree, but changes the species composition in comparison to uncut stands (Rominger, Allen-Johnson & Oldemeyer 1994). During partial harvest, removing < 30% of the total basal area maintains or will even increase the productivity of arboreal lichen; however the adjacency of early successional vegetation and forest cover may result in high quality habitat for moose and bears (Stevenson *et al.* 2001, Waterhouse *et al.* 2007, Nadeau Fortin *et al.* 2016, C Johnson Unpub Data). The reductions in arboreal and terrestrial lichen caused by harvest are disproportionately high relative to the number of trees harvested (Stevenson *et al.* 2001). Five years post-harvest, clear cuts have 25% of the terrestrial lichen of unharvested blocks, and partial cuts have 50% of the terrestrial lichen of unharvested blocks (Waterhouse 2009). In contrast, nineteen years post-harvest, partially thinned stands have higher terrestrial lichen abundance than uncut stands, and lichens were most abundant in partially thinned stands with greater canopy reductions (Vitt *et al.* 2019). However, moose may prefer partial-cut stands over clear-cut stands, potentially because they provide thermal cover and access to browse (Eastman 1974). Like wildfires, early seral vegetation produced by harvesting, and well as



specific attributes of harvested areas (e.g. partial cuts) may impact primary prey and predators (see 'Mortality'). Snow accumulation is also higher in harvested areas (Telfer 1978) which affect the foraging behavior and distribution of caribou (see 'Forage – Wildfire').

6. CONCLUSIONS

Although both wildfires and forest harvesting have negative effects on caribou habitat, forage, and population numbers, the magnitude of these effects are often higher for forestry when compared to wildfires (see Table 1 for a summary). This is especially apparent when considering caribou home ranges, habitat use, and recruitment. Forest harvesting has been linked to home range shifts, range abandonment, and reduced survival (Faille *et al.* 2010; Environment Canada 2012; Stewart *et al.* 2020; Williams *et al.* 2021). In contrast, while caribou tend to avoid wildfires at fine-scales, caribou recruitment can be relatively resilient to a high proportion of burned area within population ranges (Stewart *et al.* 2020). At fine-scales, burned and harvested areas have slightly different successional pathways, but the understory of burned versus harvested stands become similar approximately 30-100 years post-disturbance (Bergeron & Dubue 1988; Hart & Chen 2008).

With an increasing focus on ecosystem based management across the boreal forest, there may be opportunities to implement forest harvesting and silvicultural approaches to increase the similarities between harvested and burned stands, and to make harvested stands more suitable as caribou habitat into the future. At broad-scales, ongoing efforts to change forest harvesting within caribou ranges to an aggregated approach may mitigate the impacts of forest harvesting on caribou. At fine-scales, adjusting the timing or extent of stands harvested (e.g. winter harvest, partial cuts), and adapting silvicultural practices (e.g., site preparation) may reduce the differences between harvested and burned stands of equivalent ages. However, understory vegetation and the timing of succession after disturbance differs across natural subregions, ecosites, and even among microsites within stands (see 'Forage'). Detailed knowledge of how understory vegetation dynamics differ across both ecosite strata and silvicultural practices will help to inform fine-scale forest management within caribou population ranges, and is the focus of the current study. This information, together with how understory vegetation dynamics and other abiotic factors (temperature, snow) are linked to use of stands by caribou, primary prey, and predators will provide important information to inform sustainable forest management and caribou recovery efforts in Alberta.



Table 1: Summary of responses of caribou and caribou forage to wildfires and forestry across Canada, based on published and grey literature.

Habitat selection, home ranges, and movement	
	Wildfire <ul style="list-style-type: none"> Do not change home ranges in response to wildfires, avoid burned habitat in home ranges. In some areas caribou select burned habitat during summer and select wildfire residuals. Open canopy in burned habitat likely impacts movements and access to forage during winter.
	Forestry <ul style="list-style-type: none"> Shift or abandon home ranges in response to harvesting. Home range shift may lag 5-20 years after harvesting. Avoid harvested areas at broad scales, and avoid areas being actively harvested at fine scales. Females with calves select harvest blocks < 20 years old during summer in some areas. Caribou moving between intact stands among harvest blocks are at increased predation risk. Caribou may avoid partial cut harvest less than clear cut harvest, but partial cut harvest is also preferred by primary prey (moose). Open canopy after harvesting likely impacts movements and access to forage during winter.
Demography	
	Wildfire <ul style="list-style-type: none"> No direct links between wildfires and caribou mortalities, but wildfires increase caribou-predator overlap and may contribute to mortality risk at broad scales (by providing early seral habitat and increasing primary prey and predators). Accounts for 5% of variation in boreal caribou recruitment across Canada. May not impact caribou recruitment < 5 years after burning, but calf:cow ratios decrease with increasing area burned. Recruitment may be resilient to wildfires in the absence of other disturbance.
	Forestry <ul style="list-style-type: none"> Caribou have an increased risk of predation in harvested areas when compared to unharvested areas, and are more likely to encounter predators (wolves) closer to roads. Harvesting increases the density of primary prey and predators in caribou ranges, increasing predation risk. Caribou survival decreases with increasing proportions of early and mid-seral habitat within home ranges. Anthropogenic disturbance (including harvest blocks) accounts for 65% of the variation in boreal caribou recruitment across Canada. May not impact recruitment until 5-20 years after harvesting. Caribou population declines are strongly correlated with reductions in high-quality habitat resulting from forestry and energy activities.



Forage	
	Wildfire <ul style="list-style-type: none"> ▪ Generally, stand-replacing wildfires are dominated by bryophytes and vascular plants 0-40 after burning, terrestrial lichens 40-70 years after burning, and feathermosses 70+ years after burning. ▪ Arboreal lichens are largely absent from stands until 60 years after burning, but are most abundant in stands > 100 years after burning. ▪ Successional pathways and timing of succession differ across ecosites, e.g., terrestrial lichens may dominate xeric acidic sites from 10-300 years after burning. ▪ Low-intensity wildfires impact lichens less than higher-intensity fires, but may decrease the availability of arboreal lichens closer to the ground.
	Forestry <ul style="list-style-type: none"> ▪ In the absence of ground disturbance (e.g. winter harvest, no scarification), understory vegetation (including terrestrial lichens) can persist for ~2 years after harvesting. Harvested stands are dominated by vascular plants 7-25 years after harvest and successional pathways begin to converge with those of wildfires after ~30 years. ▪ Arboreal lichens are absent from harvested stands until 60-100 years after harvest. ▪ Successional pathways and timing of succession differ across ecosites. ▪ Winter harvest on snow in the absence of scarification impacts terrestrial lichens less than summer harvesting. Scarification has differing impacts on vascular plants. ▪ Herbicide application can decrease terrestrial lichen diversity and abundance. ▪ Partial cut harvesting may maintain or augment terrestrial and arboreal lichens, but may also increase habitat quality for moose.



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