



Cut vs. fire: a comparative study of the temporal effects of timber harvest and wildfire on ecological indicators of the boreal forest

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Abstract

Context Large-scale natural disturbances are crucial drivers of ecosystem function and composition for many forested ecosystems. In the last century, the prevalence of anthropogenic disturbances has increased across Canada's boreal forest. Habitat disturbance from timber harvest and wildfire is linked to declines of boreal species, including woodland caribou (*Rangifer tarandus caribou*).

Objectives We tested how disturbances influenced the recovery trajectory of ecological indicators of timber, biodiversity, and wildlife habitat through time following timber harvest and wildfire across the boreal forest of Alberta, Canada.

Methods During 2021 and 2022, we collected field data from 251 timber harvested and 264 burned stands (0–40 years since disturbance), as well as 256

older forest stands used by caribou (> 40 years since disturbance). Field data included metrics of stand attributes (e.g., basal area, stems per hectare), coarse woody debris (CWD), and abundance of forage for caribou, moose (*Alces americanus*), and bears (black bear: *Ursus americanus*, grizzly bear: *Ursus arctos*).

Results Basal area of trees and stems per hectare recovered more quickly in timber harvest sites when compared to wildfire sites, but as time since disturbance increased there were no differences in these attributes among timber harvest, wildfire, and caribou use sites. CWD was greatest in recently burned sites, but declined over time to be similar in quantity as in harvested stands and older forest stands. Terrestrial lichens, important forage for caribou, were most abundant in the older caribou use sites, whereas forage for moose and bears, including shrubs, was most abundant in younger timber harvest and wildfire sites.

Conclusions Our results demonstrate that timber harvesting may result in a quicker development of timber volume when compared to wildfire. However, this anthropogenic disturbance is less advantageous for the development of caribou habitat.

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Introduction

Forest ecosystems in North America have long been shaped by natural disturbances, such as windstorms, insect outbreaks, and wildfire (White 1979; Dale et al. 2001; Flannigan et al. 2003). Disturbance drives successional dynamics and ecosystem function, influencing community composition, species richness, and biophysical characteristics (Attiwill 1994; Weber and Flannigan 1997; Gauthier et al. 2015a). Historically, wildfires have been the dominant stand-replacing natural disturbance type in Canada (Stocks et al. 2002; Gauthier et al. 2015b; Daniel et al. 2017). The leading anthropogenic stand-replacing disturbance is timber harvest, often in the form of clearcutting (Morgestern 2007; Pinno et al. 2021).

Timber harvest and wildfire have an extensive disturbance footprint, but their respective effects on forest ecosystems are rarely equivalent (McRae et al. 2001; Bergeron et al. 2004; Thiffault et al. 2007; Bartels et al. 2016). Tree size and age-class distributions, and structural complexity of residual forest patches may vary between timber harvest and wildfire (Hunter 1990; Mladenoff et al. 1993; DeLong and Tanner 1996), producing different ecosystem conditions and biological legacies (Franklin et al. 2007; Moussaoui et al. 2016). Additionally, the resulting composition of tree species may differ in post-harvest and post-fire stands, with the former often dominated by deciduous tree species (Carleton and MacLellan 1994; Jackson et al. 2000; Pinto et al. 2008).

Forest managers have used ecosystem-based management (EBM) to reduce the dissimilarities between natural and anthropogenic disturbances (Seymour and Hunter 1999; Bergeron et al. 2002; Harvey et al. 2002). The primary objective of EBM is to develop harvesting regimes that emulate natural disturbance (Christensen et al. 1996; Bergeron et al. 1999; Mori et al. 2013). Flora and fauna have evolved to accommodate natural disturbance dynamics (e.g., type, rate, and extent of disturbance) particular to the ecosystems that they occupy (Weber and Taylor 1992; Bunnell 1995; McRae et al. 2001). Thus, EBM assumes that ecosystem characteristics, including biodiversity, can be maintained when timber harvest replaces natural disturbance (Angelstam 1998; Seip 1998; DeLong 2007). However, to assess if EBM can be effectively applied, there needs to be a comprehensive understanding of the differential effects of timber harvest

and wildfire across relatively broad temporal and spatial extents.

Forests across Canada provide a broad suite of ecosystem services, including timber production (Burton et al. 2006, 2010). Over two-thirds of the boreal forest is managed, mainly for timber production (Gauthier et al. 2015b). Forest management generally includes harvesting or silvicultural prescriptions that are intended to promote the regeneration of commercially valuable species (Armstrong 2004; Fourrier et al. 2013; Fleming et al. 2014). Ecological indicators for timber supply often include stand attributes such as tree species composition and harvestable volume (McElhinny et al. 2005; Government of Canada 2021). In this study, we refer to stand attributes as measures of basal area, stem density, and species composition for trees, adhering to standard inventory used for forest management (Government of Alberta 2023). There is ample research on stand dynamics, such as changes in tree species composition and basal area, following timber harvest or wildfire (Greene et al. 1999; Chen and Popadiouk 2002; Haeussler and Kneeshaw 2003; Johnson et al. 2003). However, few studies have compared stand attributes and wildlife habitat of similarly aged harvested and wildfire areas in boreal forests, especially over broad temporal and geographical ranges (Hobson and Schieck 1999; Fourrier et al. 2013; Souliere et al. 2020; Yemshanov et al. 2020).

In tandem with provisioning ecosystem services, forests also provide supporting services, including habitat for a multitude of species (Burton et al. 2006; Saarikoski et al. 2015). Management practices that prioritize certain forest attributes, such as volume of merchantable timber, may reduce the availability of other supporting services (Thom and Seidl 2016). For example, harvesting of old forest can lead to habitat loss and fragmentation for woodland caribou (*Rangifer tarandus caribou*), hereafter ‘caribou’, a species listed as Threatened under Canada’s Species-At-Risk Act (Environment Canada 2011). Conversely, recently disturbed forests attract other ungulate species, such as moose (*Alces americanus*), that are associated with early seral plant communities (Johnson and Rea 2024). An increase in the distribution or abundance of moose can result in more wolves (*Canis lupus*), a shared predator of moose and caribou (DeCesare et al. 2010; Johnson et al. 2020). This process of apparent competition has contributed to the decline of

caribou across western Canada (Serrouya et al. 2011). Therefore, it is important to understand the temporal responses of a range of forest attributes, including indicators of biodiversity and wildlife habitat, following timber harvest and wildfire to effectively inform landscape management (Thom and Seidl 2016; Ihmezie et al. 2021), including habitat of wildlife like caribou.

Timber harvest and wildfire alter forest structure, but the resulting biological legacies can differ between the two disturbance types (McRae et al. 2001). Biological legacies, in the form of dead wood, are vital for supporting forest biodiversity (Huston 1996). Coarse woody debris (CWD), defined as relatively large dead woody material that is undergoing decomposition (Harmon et al. 1986; Harmon and Sexton 1996), provides suitable habitat for an array of different organisms (McMinn and Crossley 1996; Bull 2002). For example, birds and small mammals use standing dead trees, like snags, for nests, nurseries, and storing food (Farnell et al. 2020). In addition, CWD is important for nutrient cycling, long-term carbon storage, and tree regeneration (Sturtevant et al. 1997; Hagan and Grove 1999). The quantity (e.g., volume) and quality (e.g., size and decomposition stage) of CWD are influenced by ecosystem and disturbance type, as well as the successional patterns that follow (Pedlar et al. 2002). Wildfires produce standing dead trees (future downed CWD) and downed woody debris (Franklin et al. 2007; Moore 2022), whereas clearcut harvesting may remove most of the CWD, including future CWD in the form of standing dead trees (Tinker and Knight 2000; McRae et al. 2001).

Timber harvest and wildfire also influence the availability and quality of forage for a multitude of wildlife species (Burton 2013; Commander and White 2020). In western Canada, terrestrial and arboreal lichens are the preferred winter forage of caribou. (Johnson et al. 2001; Bergerud et al. 2008; Denryter et al. 2017). The abundance of lichens generally decreases following wildfire and clearcut harvesting (Ahti 1977; Coxson and Marsh 2001; Russell and Johnson 2019), although forage lichens will typically become accessible for caribou 40–50 years post-disturbance (Nguyen-Xuan et al. 2000; Joly et al. 2003;). Conversely, other more generalist, boreal ungulates, like moose, deer (*Odocoileus* spp.), and elk (*Cervus canadensis*) favor vascular plants, which

are abundant in early seral forest (Franzmann and Schwartz 1997; Visscher et al. 2006; DeCesare et al. 2010). Increases in the density of generalist ungulates may attract predators like wolves and cougars (*Puma concolor*) (Serrouya et al. 2021; McKay and Finnegan 2022). Moreover, other predators including black bears (*Ursus americanus*) and grizzly bears (*Ursus arctos*) also prefer early seral forests to access forbs and berry-producing shrubs (Latham et al. 2011; Souliere et al. 2020). An assessment of forage availability for caribou, moose, and bears following timber harvest or wildfire can be an effective indicator of the impacts of disturbance on wildlife habitat, especially for caribou as increased forage for moose and bears could reflect greater apparent competition and predation risk (DeCesare et al. 2010; Serrouya et al. 2011). Despite initial similarities in vegetation communities following timber harvest or wildfire (Coxson and Marsh 2001), the temporal changes in abundance of forage taxa may differ between these two disturbance types (Reich et al. 2001).

In this study, we compared the temporal responses of stand attributes, woody debris, and abundance of forage for caribou, moose, and bears following timber harvest and wildfire across the boreal and foothill forests of Alberta, Canada. We collected field data from forest stands that had been disturbed by timber harvest and wildfire (<40 years since disturbance), as well as older forest stands (>40 years since disturbance) representative of the habitat of woodland caribou, a high-priority conservation species found across the boreal forest in Canada. With a goal of informing effective EBM practices in the boreal forests of western Canada, our objectives were to assess the ecological indicators in relation to (1) post-disturbance temporal trends, (2) differences between site type (timber harvest vs. wildfire vs. caribou use), and (3) trends between forest ecosystem subtypes. We hypothesized (i) stand attributes would initially be similar following timber harvest or wildfire, but the successional trajectories of each disturbance type would diverge over time; (ii) CWD would be more abundant in wildfire sites compared to timber harvested sites, especially immediately after disturbance; and (iii) forage groups for moose and bears would be more abundant in recently disturbed forest (Coxson and Marsh 2001; McClelland et al. 2023), and caribou forage would be more prevalent in mature forest (Ray et al. 2015; Russell and Johnson 2019).

Materials and methods

Study area

The study area included 88,900 km² of west-central, north-western, and north-eastern Alberta, Canada (Fig. 1). Natural subregions within the study area included the central mixedwood, lower and upper foothills, and lower and upper boreal highlands (Natural Regions Committee 2006). Natural subregions are ecological units defined according to climate, topography, vegetation, and soil properties (Natural Regions Committee 2006)—representing variation in ecosystem subtype (Table 1). The study area incorporated the ranges of nine caribou populations: Chin-chaga, East Side Athabasca, West Side Athabasca, Little Smoky, Nipisi, and Red Earth (boreal caribou;

COSEWIC 2011), and À la Pêche, Narraway, and Redrock Prairie Creek (central mountain caribou; COSEWIC 2011).

The dominant tree species in the study area included lodgepole pine (*Pinus contorta*), jack pine (*Pinus banksiana*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), tamarack (*Larix laricina*), and paper birch (*Betula papyrifera*). Shrubs and forbs included willows (*Salix* spp.), bog birch (*Betula glandulosum*), alders (*Alnus* spp.), blueberries (*Vaccinium* spp.), Labrador tea (*Rhododendron groenlandicum*), and horse-tails (*Equisetum* spp.). Ungulates in the study area included caribou, moose, elk, white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), bighorn sheep (*Ovis canadensis*), and mountain

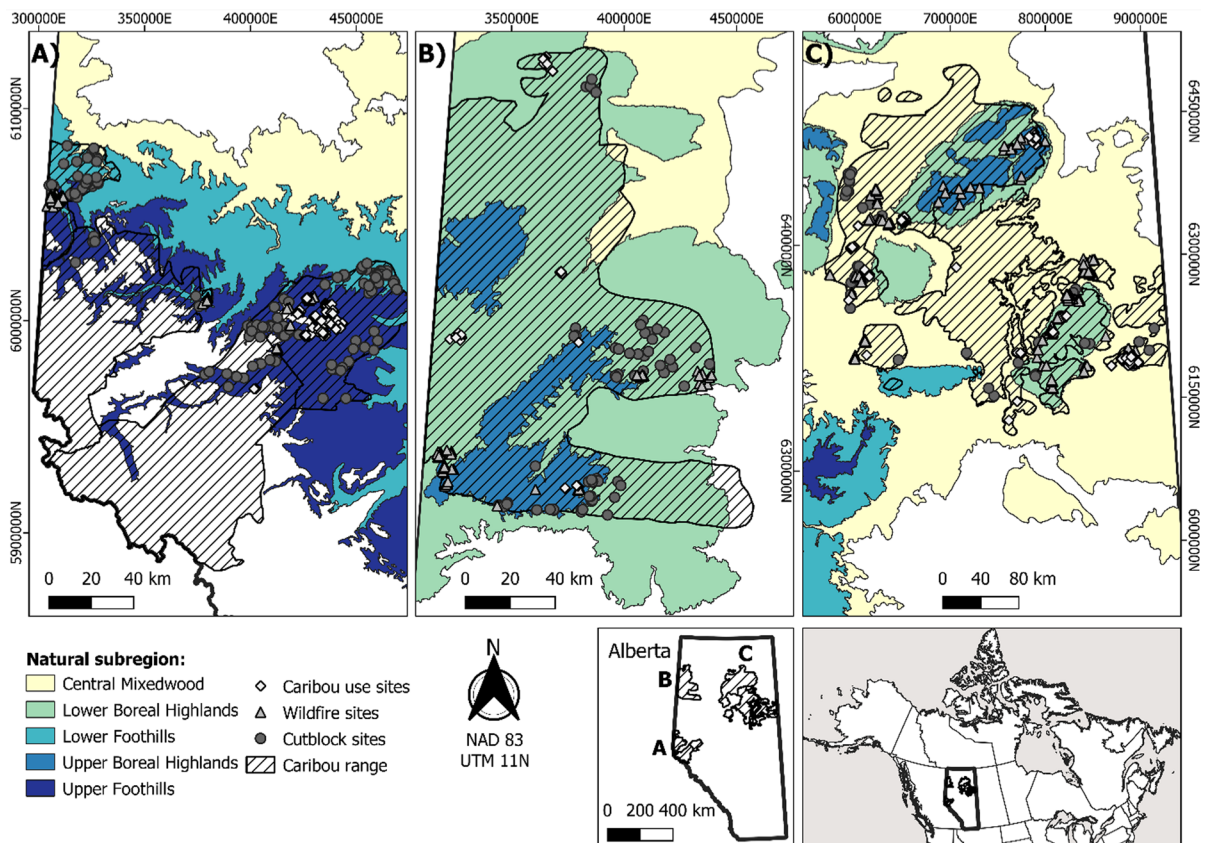


Fig. 1 Location of sampled sites across **A**) west-central, **B**) north-western, and **C**) north-eastern regions of Alberta, Canada. Natural subregions are presented in color; caribou herd range is represented by dashed lines; caribou use sites are indi-

cated by diamonds, wildfire sites by triangles, and cutblock sites by circles. Field sampling of sites was conducted during the summers of 2021 and 2022

Table 1 Characteristics of natural subregions sampled from cutblock, wildfire, and caribou use sites in Alberta, Canada, in 2021 and 2022

Natural subregion	Area (km ²) ^a	Elevation (m) ^b	Vegetation (dominant tree species)	% Wetlands	Precipitation (mm) ^c	Land use ^d
Central mixedwood	167,856	525 (200–1050)	Closed-canopy mixed-wood forests (aspen, white spruce, jack pine, black spruce)	40	478	Forestry, oil and gas, agriculture
Lower boreal highlands	55,615	675 (400–1050)	Mixed forests (aspen, balsam poplar, black and white spruce, paper birch)	30	495	Forestry, oil and gas
Upper boreal highlands	11,858	825 (650–1150)	Coniferous forests (lodgepole pine, jack pine, black spruce)	35	535	Forestry, oil and gas
Lower foothills	44,899	950 (650–1625)	Mixedwood forests (aspen, lodgepole pine, white spruce)	20	588	Forestry, oil and gas, agriculture
Upper foothills	21,537	1300 (950–1750)	Closed coniferous forests (lodgepole pine, black spruce, white spruce)	10	632	Forestry, oil and gas

Adapted from Natural Regions Committee (2006)

^aTotal area of natural subregion

^bAverages are presented for elevation with range in ()

^cMean annual precipitation of natural subregion

^dLand use with a focus on anthropogenic disturbances

goats (*Oreamnos americanus*) at higher elevations. Large carnivores included wolves, grizzly bears, black bears, cougars, Canada lynx (*Lynx canadensis*), coyotes (*Canis latrans*), and wolverines (*Gulo gulo*).

Oil and gas extraction, and timber harvest were the primary anthropogenic disturbances in the study area. Conventional clearcutting followed by planting of commercial stock was the prevalent form of timber management in these regions (Schneider 2002; Alberta Sustainable Resource Development 2006). Natural disturbance in the study area included forest pathogens, bark beetles (e.g., mountain pine beetle *Dendroctonus ponderosae*), windthrow, and wildfire.

Site selection

We selected sites to represent anthropogenic (timber harvest) and natural (wildfire) disturbances, as well as sites that were used by caribou; hereafter ‘cutblock’, ‘wildfire’, and ‘caribou use’ sites (Fig. 1). Sites were stratified by natural subregion and age class; disturbance sites (cutblock and wildfire) were grouped into

four 10-year intervals (0–10, 11–20, 21–30, 31–40) reflecting the time since disturbance. All caribou use sites were greater than 40 years since disturbance. Caribou typically select mature forest (> 40 years since disturbance) for their winter habitat (Johnson et al. 2015; Mumma et al. 2018; Rudolph et al. 2019). Sites were randomly selected within each stratum. We identified cutblock and wildfire sites using forest resource inventory and historical wildfire data provided by the Government of Alberta. Cutblock sites were clearcut harvested and wildfire sites experienced large-scale, stand-replacing wildfires (> 94% of area burned, > 200 ha burned area).

We used GPS location data (2019–2022) from collared caribou to identify caribou use sites. Caribou were collared by the Government of Alberta as part of provincial monitoring programs (Government of Alberta Wildlife Caribou Committee Class Protocol #8). First, we partitioned GPS location data into population and season (Table S1; MacNearney et al. 2016; Pigeon et al. 2016; Konkolics et al. 2021) and created a point density layer with a 500-m cell size.

Then, we assigned each cell to one of three quantiles representing a low, medium, or high density of caribou locations. Finally, we randomly selected cells from each natural subregion and season that represented areas with high-density of caribou locations, assuming that those areas had a relatively greater use by caribou. If there were insufficient high-density locations for a natural subregion then we randomly selected cells with a medium density of use. We did not draw sample sites from low-density areas.

Cutblock, wildfire, and caribou use sites were >500 m from other sites within the same strata, and >20 m from the stratum edge. Most sites were road accessible (<3 km of the nearest road), except for sites in the north-eastern region, which were only accessible via helicopter. If we encountered strata mismatches in the field (e.g., a caribou use site that had been harvested after GPS data had been collected), we moved the sampling plot by increments of 20 m in a randomly selected cardinal direction until the plot fell within the target stratum.

Field data collection

We sampled 251 cutblock, 264 wildfire, and 256 caribou use sites from early June to late August in 2021 and late May to early September in 2022. We established 100-m² fixed-diameter circular sampling plots (5.64-m radius; Fig. S1) within each site and recorded diameter at breast height (DBH), species composition, and density counts (stems/ha) for all trees with a DBH ≥ 5 cm. We recorded the status of each tree as alive, snag (dead tree ≥ 1.3 m in length, leaning $\leq 45^\circ$ from the vertical), or stump (dead tree <1.3 m high). We also recorded the density of saplings (DBH < 5 cm) by species.

We sampled CWD along four transects (5.64 m in length) within the 100-m² plot, one at each cardinal direction. Measurements of CWD included logs on the ground and downed woody material at an angle of $>45^\circ$ from the vertical, >5 cm diameter, >1 m length, and with $>50\%$ of the diameter above forest litter or soil where the logs intersected CWD transects. Due to time constraints, we employed a simplified three-class decomposition classification for CWD: type I—little to no decay with intact bark and hard wood; type II—significant decay and bark mostly gone, wood had begun to soften, but retained structure; and type III—debris was soft throughout

with a lack of structure. We counted the number of pieces of CWD intersecting each transect, identifying species when possible, and recording if the CWD was on the ground or suspended.

We measured percent cover of large shrubs within 5-m² circular plots (1.26-m radius) located at the north, east, south, and west edges of the 100-m² plot (Fig. S1, Table S2). We measured percent cover of dwarf shrubs, forbs, graminoids, terrestrial lichens, and other ground cover (Table S2) in one 1-m² circular plot (0.564-m radius) within each of the 5-m² plots (Fig. S1). All measurements of percent cover were taken to the nearest whole percent (i.e., discrete integers).

Ecological indicators

We assessed four stand attributes of trees associated with timber supply: basal area, tree type composition (basal area of only deciduous trees), quadratic mean diameter (QMD in cm), and stems per hectare (SPH) (Table 2). We calculated these attributes for live trees (DBH ≥ 5 cm), excluding snags and stumps.

We used counts of CWD and basal area of snags as indicators of stand-level biodiversity (Table 2). The measure of CWD included the total count of downed debris as well as the count of snags and stumps. This approach followed the protocol of Harmon and Sexton (1996), including debris of all decomposition classes (described in section ‘Field data collection’), suspended or on the ground, as well as standing dead trees: snags and stumps. We also calculated basal area of snags for each site. Although downed debris and standing dead trees may differ in successional state and decomposition class, they can both be important habitat for wildlife and promote biodiversity (Bull 2002).

We defined groups of plants and lichens that represented forage assemblages and components of habitat for caribou, moose, and bears (Tables 2, 3, Table S3). Winter diets of caribou are predominantly comprised of terrestrial lichens, but during spring and summer deciduous shrubs and forbs are regularly consumed (Thomas et al. 1996; Barten et al. 2001; Denryter et al. 2017). Moose browse on sapling foliage during winter but shift to shrubs and herbaceous plants during other seasons (Franzmann and Schwartz 1997; Visscher et al. 2006). Forbs and roots compose a large part of bear diet during spring and early summer,

Table 2 Variables representative of ecological indicators sampled from cutblock, wildfire, and caribou use sites in three regions in Alberta, Canada, in 2021 and 2022

Ecological indicator	Variable	Definition
Timber supply (stand attributes)	Basal area ^{a,b}	Total basal area of live trees (DBH \geq 5 cm) per site (m ² ha ⁻¹)
	Deciduous basal area ^{a,b}	Basal area of live deciduous trees (DBH \geq 5 cm) per site (m ² ha ⁻¹)
	Quadratic mean diameter (QMD) ^a	Quadratic mean diameter of trees in a site (cm)
	Stems per hectare (SPH) ^{a,b}	Total stems per hectare of trees per site (trees ha ⁻¹)
Biodiversity (woody debris)	Coarse woody debris (CWD)	Total counts of downed debris (all classes; suspended or on ground) and standing dead trees (snags, stumps) per site
	Snag basal area ^b	Basal area of snags (DBH \geq 5 cm) per site (m ² ha ⁻¹)
Wildlife habitat (forage)	Caribou (lichens, forbs) ^c	Percent cover of forage items (plant/ lichen taxa)
	Moose (saplings, shrubs, forbs) ^{c,d}	Percent cover/ total count of forage items (plant taxa)
	Bear (shrubs, forbs) ^c	Percent cover of forage items (plant taxa)

^aOnly included live trees in measurements (excluded snags and stumps)

^bExtrapolated to the hectare scale

^cEach forage group defined in Table 3

^dMoose sapling forage group based on count data

while fruiting shrubs are more important during late summer and fall (Munro et al. 2006; Merkle et al. 2017). For forage groups including lichens, large shrubs, or forbs (Table 3), we summed the percent cover of all plant taxa within a given group, then calculated mean percent cover for each group across the four subplots within each 100-m² plot. For saplings (Table 3), we summed stem counts of the target species within each 100-m² plot.

Data analysis

We used two statistical approaches to quantify the relationship between disturbance type and ecological indicator. First, we used non-metric multidimensional scaling (NMDS) to explore patterns in stand attributes and forage groups within each natural subregion (Kruskal 1964). NMDS is an effective ordination method to visualize various types of data, often abundance data, in a reduced dimensional space (Kruskal 1964; Dexter et al. 2018). We used the metaMDS function (“Vegan” package, Oksanen et al. 2022) to generate separate NMDS models for stand attribute and forage group variables. For stand attributes, we first normalized the variables, and we used Euclidean distances to measure dissimilarity among the variables in NMDS. For forage groups, we used Bray distances to measure dissimilarity among the variables (Clarke 1993). For all NMDS, we used the default

of 20 re-tests to ensure confidence in the patterns of ordination (Oksanen et al. 2022). Since we were using NMDS to visualize data in a reduced dimensional space, we used two dimensions for all NMDS. We used a stress value threshold of 0.20 to evaluate the goodness of fit for each NMDS; with values above 0.20 indicating a poor fit, values below 0.20 indicating a decent fit, and values below 0.10 indicating a good fit (Kruskal 1964; Clarke 1993). We grouped data by the stratum ‘disturbance type’ to visualize potential clustering or separation of the indicators with disturbance type. We excluded the woody debris variables from ordination analysis, as there were only two variables and we wanted to analyze them separately because they were neither stand attribute nor forage group.

We used generalized linear models (GLM) to explore the relationship between ecological indicators and disturbance type. We used Gaussian linear regression (link = identity) to model stand attributes and snag basal area. The CWD and forage group variables were overdispersed, thus, we used negative binomial count models (link = log) for those variables (“MASS” package, Venables and Ripley 2002). For the forage group variables measured in percent cover, although these data were not discrete integers after calculating mean values for each site, they were still non-negative with overdispersed distributions best suited for negative binomial count models (Zuur et al.

Table 3 Description of forage groups for caribou (*Rangifer tarandus caribou*), moose (*Alces americanus*), and bears (black bear: *Ursus americanus*, grizzly bear: *U. arctos*) found across western Canada

Wildlife	Forage group	Plant/lichen taxa (scientific name)	Plot size (m ²)	Site mean abundance	References
Caribou	Terrestrial lichens (caribou lichens)	Iceland lichen (<i>Cetraria</i> spp.)	1	0.078 ^a	Denryter et al. (2017), Russell and Johnson (2019) and Nobert et al. (2020)
		Reindeer lichen (<i>Cladonia</i> spp.)	1	2.937 ^a	
		Cup lichen (<i>Cladonia</i> spp.)	1	1.563 ^a	
		Ragged lichen (<i>Flavoce-traria</i> spp.)	1	0.054 ^a	
	Dwarf shrubs/forbs ^c (caribou forbs)	Hairy wildrye (<i>Elymus innovates</i>)	1	0.406 ^a	
		Creamy peavine (<i>Lathyrus ochroleucus</i>)	1	0.126 ^a	
		Clover (<i>Trifolium</i> spp.)	1	0.030 ^a	
Moose	Saplings (moose saplings)	Blueberries (<i>Vaccinium</i> spp.)	1	3.999 ^a	Franzmann and Schwartz (1997), Strong and Gates (2006) and Koetke et al. (2023)
		Balsam fir (<i>Abies balsamea</i>)	100	0.263 ^b	
		Subalpine fir (<i>Abies lasiocarpa</i>)	100	4.634 ^b	
		Paper birch (<i>Betula papyrifera</i>)	100	1.201 ^b	
		Balsam poplar (<i>Populus balsamifera</i>)	100	2.876 ^b	
	Large shrubs (moose shrubs)	Trembling aspen (<i>Populus tremuloides</i>)	100	14.197 ^b	
		Saskatoon (<i>Amelanchier alnifolia</i>)	5	0.063 ^a	
		Red osier dogwood (<i>Cornus stolonifera</i>)	5	0.023 ^a	
		Chokecherry (<i>Prunus virginiana</i>)	5	0.008 ^a	
		Willows (<i>Salix</i> spp.)	5	3.362 ^a	
	Dwarf shrubs/forbs ^c (moose forbs)	Low bush cranberry (<i>Viburnum edule</i>)	5	0.676 ^a	
		Sarsaparilla (<i>Aralia nudicaulis</i>)	1	0.328 ^a	
		Sedge (<i>Carex</i> spp.)	1	2.287 ^a	
		Fireweed (<i>Chamerion</i> spp.)	1	1.287 ^a	
Bunchberry (<i>Cornus canadensis</i>)		1	2.546 ^a		
	Labrador tea (<i>Rhododendron groenlandicum</i>)	1	6.524 ^a		
	Raspberry (<i>Rubus idaeus</i>)	1	0.595 ^a		

Table 3 (continued)

Wildlife	Forage group	Plant/lichen taxa (scientific name)	Plot size (m ²)	Site mean abundance	References
Bear (Black/Grizzly)	Large shrubs/berries (bear shrubs)	Gooseberries/ currants (<i>Ribes</i> spp.)	5	0.219a	Nielsen et al. (2004), Munro et al. (2006), Merkle et al. (2017) and McClelland et al. (2023)
		Bracted honeysuckle (<i>Lonicera involucrata</i>)	5	0.321 ^a	
		Buffaloberry (<i>Shepherdia canadensis</i>)	5	0.094 ^a	
		Low bush cranberry (<i>Viburnum edule</i>)	5	0.676 ^a	
	Dwarf shrubs/forbs (bear forbs)	Sarsaparilla (<i>Aralia nudicaulis</i>)	1	0.328 ^a	
		Horsetails (<i>Equisetum</i> spp.)	1	2.135 ^a	
		Raspberry (<i>Rubus idaeus</i>)	1	0.595 ^a	
		Clover (<i>Trifolium</i> spp.)	1	0.030 ^a	
		Blueberries (<i>Vaccinium</i> spp.)	1	3.999 ^a	
		Lingon berry (<i>Vaccinium vitis-idaea</i>)	1	3.294 ^a	

Plant taxa, sampling plot size, and site mean abundance are listed. Forage groups were comprised of plant or lichen taxa documented to be important forage items for each wildlife species. Plant taxa were also grouped together based on sampling method (e.g., plot size)

^aAbundance = mean percent cover

^bAbundance = mean count

^cForage group also includes graminoid species

2010; Stoklosa et al. 2022). Therefore, to better align with the requirements of count models, we rounded these percentage values to the nearest whole number (Russell and Johnson 2019). Also, for plots with mean values between 0 and 0.5, we rounded up to 1 to ensure that we did not underrepresent presence of forage among sites. We developed a categorical variable ‘disturbance class’ to include all possible subgroups of ‘disturbance type’ and ‘time since disturbance’ (0–10, 11–20, 21–30, 31–40, > 40 years) within models. The ‘disturbance class’ factor included the levels: cutblock 0–10, wildfire 0–10, cutblock 11–20, wildfire 11–20, cutblock 21–30, wildfire 21–30, cutblock 31–40, wildfire 31–40, caribou use > 40. The development of the disturbance class variable enabled us to compare all age classes of the cutblock and wildfire sites to the caribou use sites (caribou use sites all > 40 years). We included disturbance class as a factor in all GLMs, with ‘caribou use > 40’ as the reference category. We scaled each stand attribute variable included

in the linear regression models using the scale function in base R. We used the residuals of the linear regression models to confirm normality for stand attribute variables.

We built separate models for each natural subregion, except for the lower and upper foothills where we pooled data due to insufficient sample sizes for some strata (e.g., 0 caribou use sites in the lower foothills).

We considered results statistically significant at $\alpha = 0.05$. We performed all statistical analyses using R v. 4.1.3 (R Development Core Team, 2022).

Results

Patterns of ordination

The stress values from the NMDS for stand attributes were below the threshold value of 0.20 in all

natural subregions, suggesting a good representation in reduced dimensions (central mixedwood=0.041, foothills=0.048, lower boreal highlands=0.046, upper boreal highlands=0.039). In each natural subregion, there was considerable overlap in stand attributes among cutblock, wildfire, and caribou use sites, especially between cutblock and wildfire sites (Fig. 2). Basal area and QMD were associated with caribou use sites in the foothills and lower boreal highlands based on the direction of the vectors (Fig. 2).

The stress values for forage groups were below the threshold value of 0.20 in all natural subregions, indicating acceptable fit for the representation (central mixedwood=0.186, foothills=0.148, lower boreal highlands=0.190, upper boreal highlands=0.174). In the central mixedwood and foothills, there was some separation of caribou use sites from cutblock and wildfire sites (Fig. 3). In all natural subregions, the vectors suggest that abundance of caribou lichen was associated with caribou use sites, and moose shrubs and bear shrubs were associated with cutblock sites (Fig. 3).

Impact of disturbances on ecological indicators

Following both timber harvest and wildfire, stand basal area, SPH, and QMD increased through time, and, in most natural subregions approached or exceeded the values observed in caribou use sites by 31–40 years post-disturbance (Figs. 4, 5, Fig. S2, Tables S6, S8, S9). Immediately following both timber harvest and wildfire SPH was low, but increased by 20 years post-disturbance as regenerating trees grew to exceed the lower size limit ($DBH \geq 5$ cm; Fig. 4c). In the lower and upper boreal highlands, and the central mixedwood, basal area and SPH were greater in cutblocks than in wildfire sites, particularly during early stand development (0–30 years post-disturbance). Deciduous basal area was generally low in caribou use sites in the foothills, and lower and upper boreal highlands (Fig. 4b). By 21–30 years post-disturbance, basal area of deciduous trees was greater in cutblock sites compared to caribou use sites (Figs. 4b, 5, Table S7). In contrast, basal area of deciduous trees in wildfire sites was not different from the caribou use sites, for all age classes (Figs. 4b, 5). A large

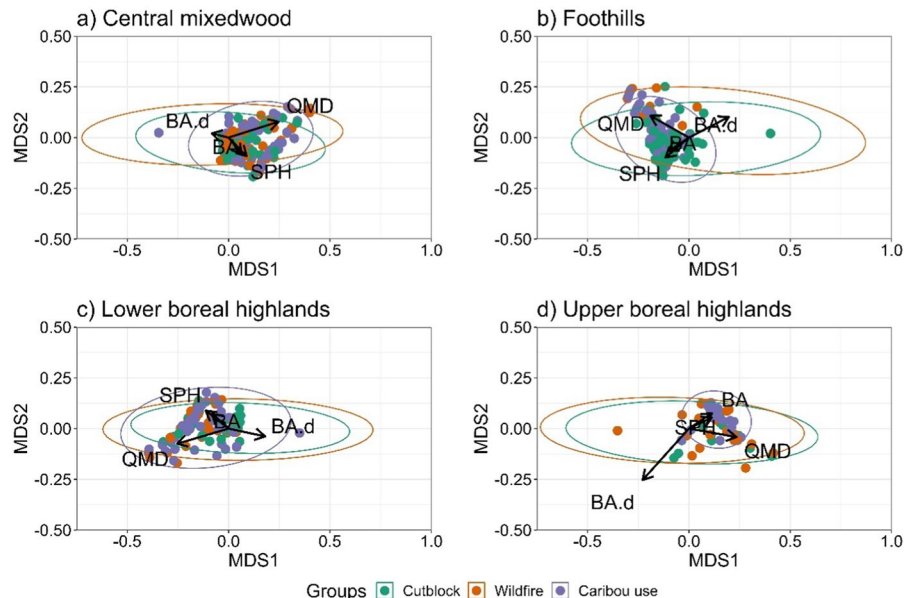


Fig. 2 Ordination from non-metric multidimensional scaling (NMDS) of stand attributes of the natural subregions: **a** central mixedwood, **b** foothills, **c** lower boreal highlands, and **d** upper boreal highlands of cutblock, wildfire, and caribou use sites sampled across natural subregions in Alberta, Canada in 2021 and 2022. BA=basal area, BA.d=deciduous basal area,

QMD=quadratic mean diameter, SPH=stems per hectare. Grouped by disturbance type; green, orange, and purple points represent cutblock, wildfire, and caribou use sites, respectively. The ellipses represent the dispersion of the data within a given group; the greater the ellipse the greater the variability

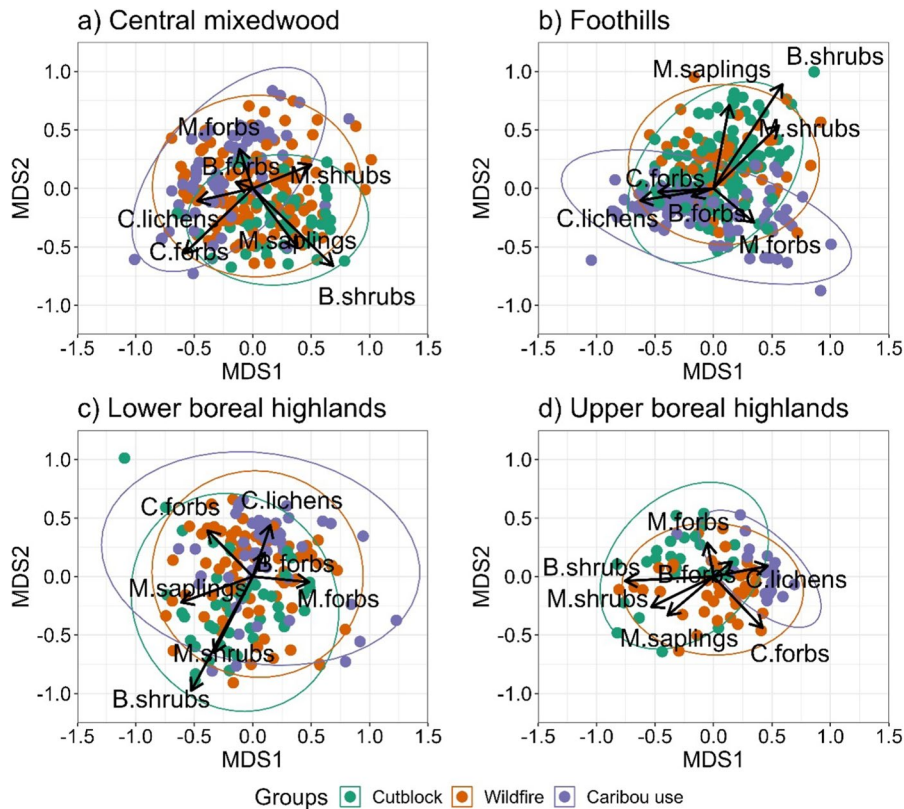


Fig. 3 Ordination from non-metric multidimensional scaling (NMDS) of forage groups of the natural subregions: **a** central mixedwood, **b** foothills, **c** lower boreal highlands, and **d** upper boreal highlands of cutblock, wildfire, and caribou use sites sampled across natural subregions in Alberta, Canada in 2021 and 2022. C.lichens=caribou lichens, C.forbs=caribou forbs, M.saplings=moose saplings, M.shrubs=moose shrubs,

M.forbs=moose forbs, B.shrubs=bear shrubs, B.forbs=bear forbs. Grouped by disturbance type; green, orange, and purple points represent cutblock, wildfire, and caribou use sites, respectively. The ellipses represent the dispersion of the data within a given group; the greater the ellipse the greater the variability

proportion of the deciduous trees were comprised of trembling aspen (Fig. S7).

CWD was more abundant in wildfire sites compared to caribou use and cutblock sites until at least 20 years post-disturbance (Figs. 4d, 5, Table S10). In all natural subregions, wildfire resulted in high initial amounts of CWD which then decreased over time, and by 31–40 years post-disturbance CWD in wildfire and caribou use sites were not significantly different from one another (Figs. 4d, 5, Table S10). Snag basal area was greater in wildfire sites than in caribou use sites until at least 10 years post-disturbance (Fig. 5, Fig. S3, Table S11). In the foothills, basal area of snags was significantly less in all age classes of cutblocks than caribou use sites (Fig. 5, Fig. S3, Table S11).

For forage groups, caribou shrubs and moose shrubs were highly correlated (Spearman $r=0.795$; Table S4), so only results of moose shrubs are reported. Caribou lichens were less abundant in cutblock than in caribou use sites, particularly in the central mixedwood and lower and upper boreal highlands (Figs. 6a, 7, Table S12). Caribou lichens were also less abundant in wildfire sites 0–10 years post-disturbance in all natural subregions (Figs. 6a, 7). Compared to cutblock sites, caribou lichens were generally more abundant in wildfire sites by 11–20 years post-disturbance (Fig. 6a). There were no clear trends in the abundance of caribou forbs among natural subregions or site types (Fig. 7, Fig. S4, Table S13).

In all natural subregions, moose saplings were generally less frequent in caribou use sites than in

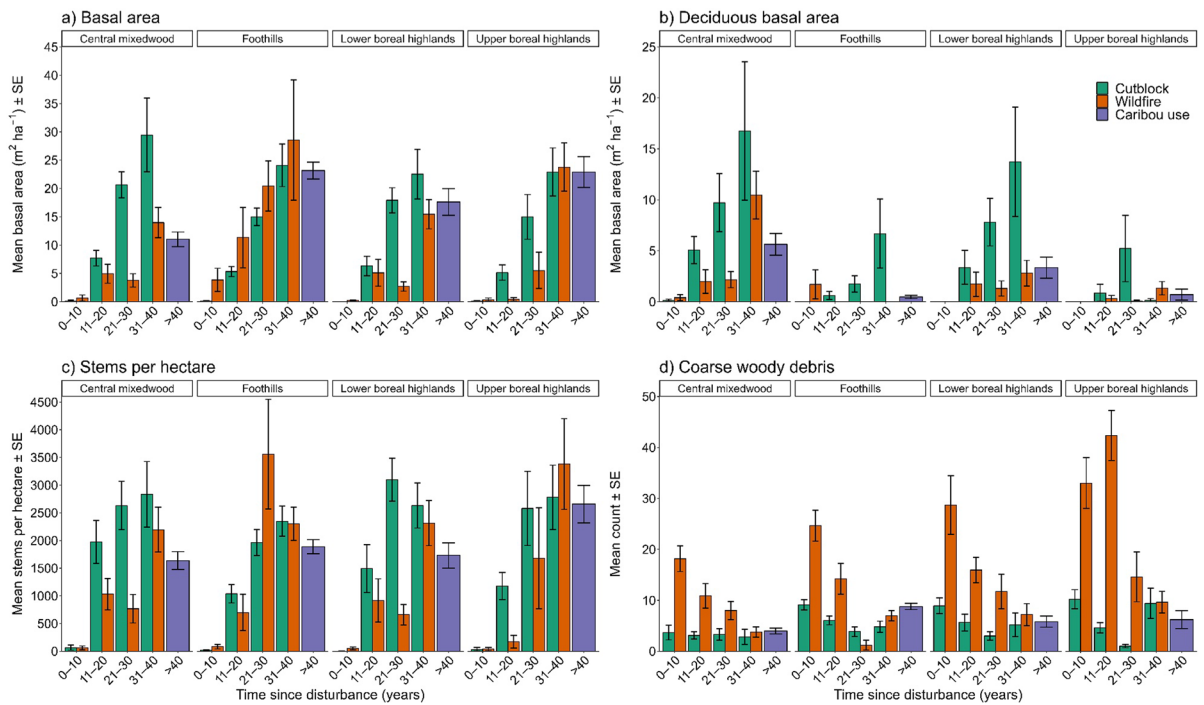


Fig. 4 Mean values of stand attributes **a** basal area, **b** deciduous basal area, **c** stems per hectare, and **d** coarse woody debris (CWD) compared between disturbance class (disturbance type

and time since disturbance) sampled across natural subregions in Alberta, Canada in 2021 and 2022. Error bars represent standard error of the mean

cutblock and wildfire sites, where abundance of this forage decreased with increased time since disturbance (Figs. 6b, 7, Table S14). In the foothills, both moose shrubs and forbs were more abundant in cutblocks compared to caribou use sites, regardless of time since disturbance (Figs. 6c, 7, Fig. S5, Tables S15, S16). Moose shrubs were also more abundant in wildfire sites when compared to caribou use sites in the central mixedwood and upper boreal highlands (Figs. 6c, 7).

Bear shrubs were more abundant in cutblock sites when compared to caribou use sites in the central mixedwood and foothills, irrespective of time since disturbance (Figs. 6d, 7, Table S17). Bear shrubs were not observed in caribou use sites in the upper boreal highlands preventing statistical comparison with disturbance type. The abundance of bear forbs

did not differ between natural subregion or site type (Fig. 7, Fig. S6, Table S18).

Discussion

The findings of this study confirm that timber harvest and wildfire produce similar outcomes for some ecological indicators but diverge substantively for others. For example, stand attributes important for timber supply regenerated quicker in cutblocks compared to wildfire sites, especially hardwood species like aspen. These results align with Fourrier et al. (2013) who found differences in merchantable timber volume and tree species composition when comparing post-harvest and post-wildfire stands in boreal forests of eastern Quebec, Canada. We found that CWD was more abundant post-wildfire. Additionally, young cutblock and wildfire sites provided ample forage for moose and bears, but both disturbance types greatly diminished the availability of terrestrial lichens—important forage for caribou. Another study conducted in west-central Alberta found that forage availability

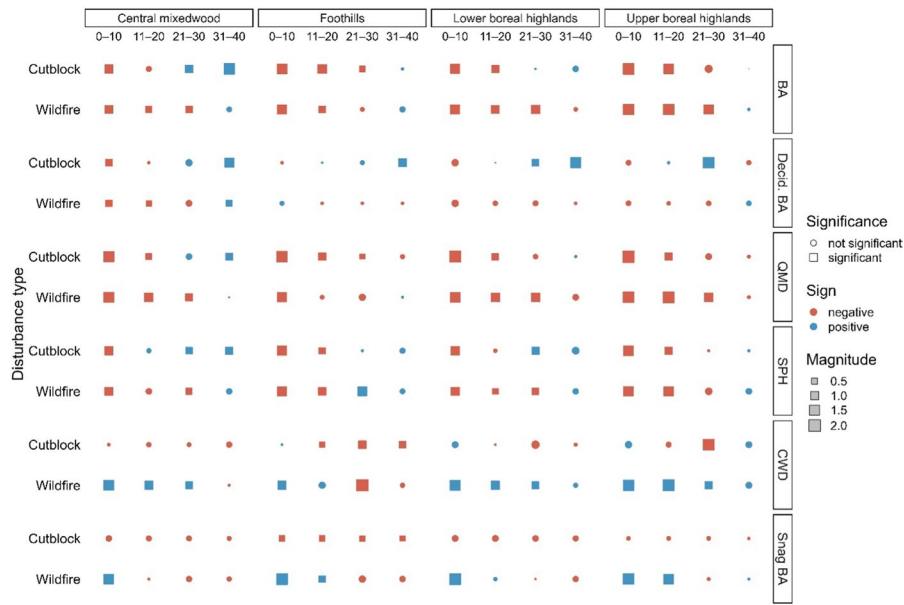


Fig. 5 Magnitude and significance of coefficients representing the effect of disturbance type and time since disturbance (disturbance class) on stand attributes, coarse woody debris, and snag basal area according to natural subregions (central mixedwood, foothills, lower boreal highlands, upper boreal highlands) in Alberta, Canada. Reference category is strata ‘Caribou use > 40 years.’ BA = basal area, Decid. BA = deciduous basal area, QMD = quadratic mean diameter, SPH = stems per hectare, CWD = coarse woody debris, Snag BA = snag

basal area. Numbers in strips at top of figure refer to time since disturbance (in years). Circles represent non-significant effects, squares represent significant effects. Red and blue symbols indicate negative and positive coefficient estimates, respectively. Size of symbol represents the magnitude of the coefficient estimate. Coefficient estimates and corresponding p-values were derived from linear models; CWD estimate from a negative binomial GLM

for grizzly bears was greatest in young age classes of both harvested and burned stands (Souliere et al. 2020). Our work also suggested that the effects of timber harvest and wildfire differed between ecosystem subtypes. For example, composition of tree species differed between the central mixedwood and foothills following disturbance. These results indicate that disturbance type and ecosystem subtype need to be jointly considered when developing goals for forest management. In our study, we covered an ecologically diverse area and assessed a range of indicators for forest products, biodiversity, and habitat for multiple wildlife.

The NMDS visualization suggested a lack of clustering or association of stand attributes relative to the disturbance groups (cutblock, wildfire, caribou use). This could be because time since disturbance was not included in the ordination. After a clearcut or severe wildfire the remnant basal area and stems per hectare would likely be much less than in more mature stands (Greene et al. 1999; Madoui et al. 2015). There was

some degree of separation between forage groups and disturbance type, mainly characterized by caribou lichens within the caribou use group, and moose and bear shrubs within the cutblock group. These results are not surprising as terrestrial lichens are typically more abundant in mature than in young forests (Ray et al. 2015; Russell and Johnson 2019), and vascular plants are more prevalent in younger, recently disturbed forest, like cutblocks, than in mature, closed canopy forest (Larsen et al. 2019; Schrempf et al. 2019; McClelland et al. 2023). The paucity of clear findings from the ordination analysis reinforced the need for us to carry out in-depth analyses incorporating time since disturbance.

Impact of disturbances on ecological indicators

In many of the natural subregions, basal area, QMD, and SPH increased more rapidly in cutblocks versus wildfire sites, which may have reflected differences in commercial tree restocking between the

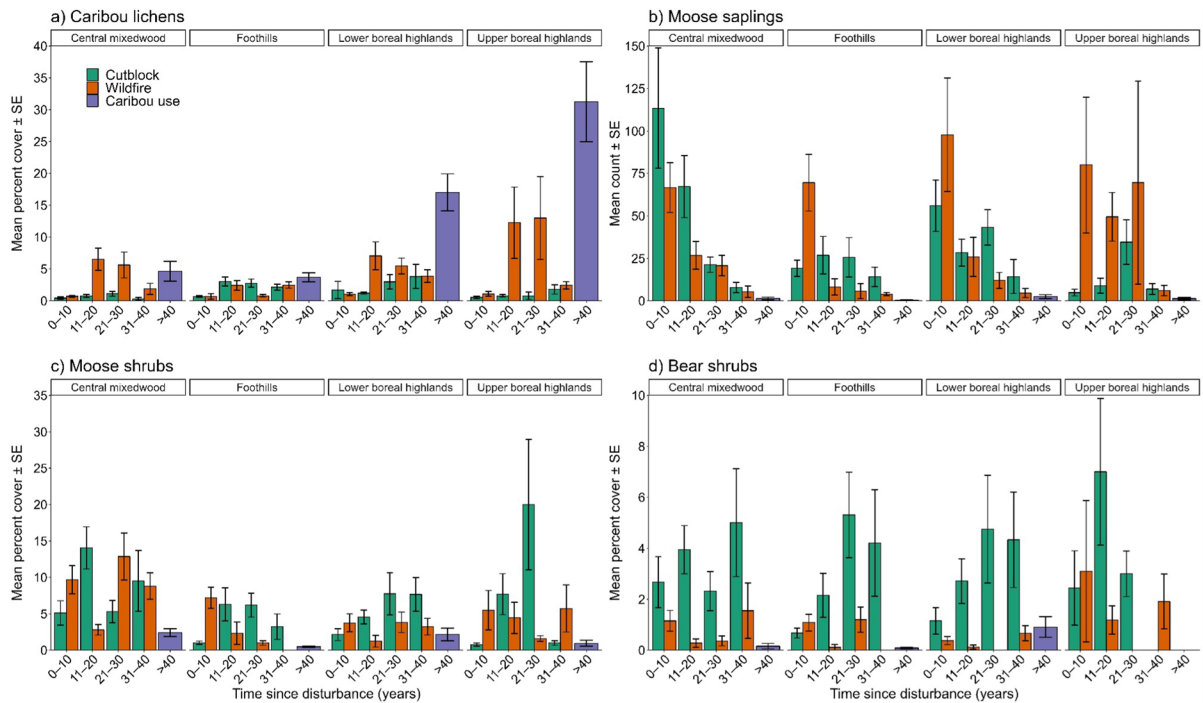


Fig. 6 Mean values of forage groups **a** caribou lichens, **b** moose saplings, **c** moose shrubs, and **d** bear shrubs compared between disturbance class (disturbance type and time since dis-

turbance) sampled across natural subregions in Alberta, Canada in 2021 and 2022. Error bars represent standard error of the mean

two disturbance types (Alberta Sustainable Resource Development 2006; Yang et al. 2008; Pinno et al. 2021). We also found that basal area of deciduous trees was generally greater in the timber harvest sites, especially in the central mixedwood and lower boreal highlands. This result suggested that highly competitive broad-leaved species, such as aspen, became established via restocking and/or natural regeneration (Chen et al. 2009; Alberta Agriculture and Forestry 2023; Bartels et al. 2016). A study by Ilisson and Chen (2009) conducted in the boreal mixedwood of Ontario found that trembling aspen and paper birch were the most abundant trees post-disturbance. In our study area, fewer biological legacies (e.g., snags, stumps, downed debris) in cutblocks could have resulted in increased light and growing space, encouraging rapid regeneration of shade-intolerant, pioneer tree species, such as aspen and birch (Greene et al. 1999; Ilisson and Chen 2009). In contrast, the prevalence of fire-remnant tree structures and exposure of mineral soil in young wildfire sites may have provided seed sources and fertile soil that facilitated the regeneration of pre-disturbance species, including

conifers (Carleton and MacLellan 1994; Greene et al. 1999; Franklin et al. 2002).

We found that counts of CWD and basal area of snags were most abundant in the young wildfire sites. This was consistent across natural subregions and in accordance with other studies (Tinker and Knight 2000; McRae et al. 2001; Yan et al. 2007; Moore 2022). For example, in forested areas of northwestern Wyoming the combined mass of downed CWD and snags was almost double in burned stands compared to clearcuts (Tinker and Knight 2000). We observed high initial inputs of standing dead trees and downed debris and then a decrease in CWD over time in the wildfire sites, which matched the initial stages of the “u-shaped” temporal trend (Sturtevant et al. 1997; Feller 2003; Yan et al. 2007). The low abundance of CWD we observed in cutblocks was likely due to timber harvest practices removing standing dead trees and downed woody debris (Hagan and Grove 1999; Schneider 2002; Alberta Sustainable Resource Development 2006). The absence of CWD in timber harvest sites likely reduced habitat availability for many taxa (Huston 1996; McMinn and Crossley 1996;

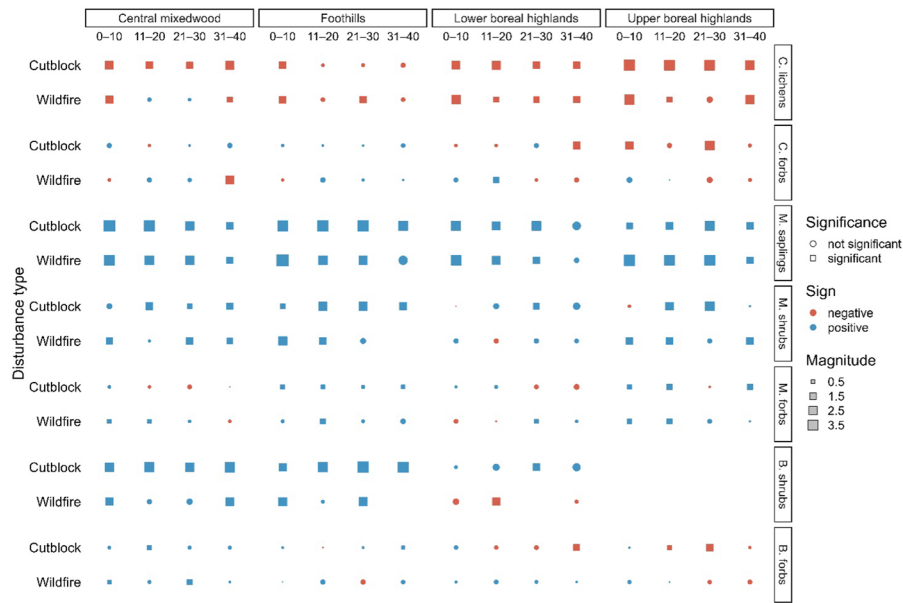


Fig. 7 Magnitude and significance of coefficients representing the effect of disturbance type and time since disturbance (disturbance class) on forage groups according to natural subregions (central mixedwood, foothills, lower boreal highlands, upper boreal highlands) in Alberta, Canada. Reference category is strata ‘Caribou use > 40 years.’ C. lichens = caribou lichens, C. forbs = caribou forbs, M. saplings = moose saplings, M. shrubs = moose shrubs, M. forbs = moose forbs, B. shrubs = bear shrubs, B. forbs = bear forbs; Numbers in strips at top of figure refer to time since disturbance (in years). Circles represent non-significant effects, squares represent sig-

nificant effects. Red and blue symbols indicate negative and positive coefficient estimates, respectively. Size of symbol represents the magnitude of the coefficient estimate. Coefficient estimates and corresponding p-values were derived from negative binomial GLMs. Moose shrubs (M. shrubs) did not occur in ‘Wildfire 31–40’ strata in foothills, and Bear shrubs (B. shrubs) did not occur in ‘Wildfire 31–40’ strata in foothills, ‘Wildfire 21–30’ strata in lower boreal highlands, and reference category sites (Caribou use > 40) in upper boreal highlands, therefore the respective coefficient estimates were omitted

Bull 2002). Our assessment of CWD only included counts, as well as basal area of snags, not measures of biomass or volume, and we adopted a simplified decomposition scale to be more time efficient during the field surveys. Given that relatively simplistic sampling protocol, we may not have fully captured all fine-scale variation in the abundance and attributes of CWD (Harmon and Sexton 1996; Yan et al. 2007). However, even with a less rigorous sampling protocol, we still found differences in abundance of CWD among disturbance types, consistent with our hypothesis that counts of CWD would be greatest in recently burned stands.

Abundance of caribou lichens was greatest in the older caribou use sites, and substantively less in cutblock and wildfire sites for at least 10 years following disturbance across all natural subregions. Moreover, percent cover of caribou lichens was scarce in cutblocks for up to 40 years post-harvest. Typically, a

large proportion of terrestrial lichens is destroyed following severe, large-scale disturbance events (Dunford et al. 2006; Ray et al. 2015; Cichowski et al. 2022) and it can take from 40 to over 70 years for lichens to regenerate (Brulisauer et al. 1996; Waterhouse et al. 2011; Russell and Johnson 2019). We also found differences among natural subregions. In the central mixedwood and upper and lower boreal highlands, percent cover of caribou lichens was greater in wildfire sites compared to cutblocks 10 years post-disturbance. Nobert et al. (2020), working in the boreal highlands of Alberta, also found terrestrial lichens were more abundant following wildfire when compared to timber harvest. When compared to other natural subregions, we found caribou lichens were less abundant in caribou use sites in the central mixedwood and foothills, which may be explained by wetter edaphic conditions and closed canopies typical of those natural subregions (Table 1; Natural Regions

Committee 2006). Lichen growth can be limited by mosses and vascular plants that benefit from moist, productive soil conditions (Coxson and Marsh 2001; Nobert et al. 2020; Cichowski et al. 2022).

Consistent with our hypothesis, and previous research (Strong and Gates 2006; McKay and Finnegan 2023), both moose saplings and shrubs were more abundant in the young timber harvest and wildfire sites compared to the caribou use sites. We observed a decrease in the abundance of moose saplings over time, which corresponded with observed successional patterns for the plant species associated with this forage group in boreal forests (Chen and Popadiouk 2002; Bartels et al. 2016).

We found that bear shrubs were most abundant in cutblocks, with significant differences detected across natural subregions between cutblocks of various age classes and caribou use sites. Our results were consistent with other studies that found fruit-bearing shrubs preferred by bears were abundant in stands following timber harvest (Nielsen et al. 2004; Souliere et al. 2020; Colton et al. 2021). We found that both moose and bear shrubs were sparse or completely absent in caribou use sites (i.e., 0 bear shrubs in upper boreal highlands). This can be expected considering the successional patterns of shade-intolerant shrub species (Hart and Chen 2006) and highlights the different ecological niches of these wildlife species.

We did not observe many differences among disturbance type for caribou forbs, moose forbs, or bear forbs. Generally, each of these forage groups were as abundant in the different-aged disturbance sites as in the caribou use sites. All three forage groups contained a variety of shade tolerant and intolerant dwarf shrubs, forbs, and graminoids that were prevalent during different successional stages (Humbert et al. 2007).

Implications for ecosystem management

We investigated differences in the temporal responses of a range of ecological indicators following timber harvest and wildfire. Focusing on stand attributes related to merchantable timber, we found that by 20 years post-disturbance, basal area, QMD, and SPH in cutblock sites generally reached or even exceeded the amounts in the more mature caribou use sites. This general trend was not observed in the wildfire sites. From the perspective of timber production,

forest growth following timber harvest was better than following wildfire. However, greater timber production was expected as those sites likely received silvicultural treatment including planting of commercial seedlings and treatments to reduce competition from brush (Schneider 2002; Pinno et al. 2021).

Timber harvest was not the most advantageous disturbance type for the full set of ecological indicators that we assessed. For example, caribou lichens were sparse in cutblocks and generally increased more quickly after disturbance in wildfire sites. Similarly, we found that CWD abundance was greater in recently burned stands compared to timber harvested ones. In our study area, post-harvest site preparation typically included the removal of dead woody structures that served as habitat for a broad range of biodiversity (Huston 1996; McRae et al. 2001; Bull 2002). Following from EBM, if timber harvest is striving to emulate wildfire, then efforts should be made to retain standing dead trees and downed woody debris (Franklin et al. 2002; Lindenmayer et al. 2012). The retention of both living and dead trees will provide habitat, now and in the future, for biodiversity that is dependent on CWD (Gustafsson et al. 2012; Fedrowitz et al. 2014).

Timber harvest and wildfire remove overstory canopy, promoting the growth of early seral vegetation, such as forbs, shrubs, and saplings (Bergqvist et al. 2018; Schrempf et al. 2019). Although early seral forest resulting from timber harvest produces forage for caribou, moose, and bears, roads built alongside harvesting operations can increase human access, and facilitate predator movement (e.g., wolves) (Serrouya et al. 2017; Mumma et al. 2018, 2019). Caribou face even greater risks when early seral forest attracts apparent competitors (e.g., moose, deer, elk) and their predators (DeCesare et al. 2010; Serrouya et al. 2021).

Our results suggest that neither timber harvest nor wildfire will provide favorable outcomes for the full set of ecological indicators across the boreal forest and temporal period that we studied. Furthermore, the effects of timber harvest and wildfire are not always interchangeable, and these effects may vary between ecosystem subtypes. For instance, timber harvest resulted in a greater production of merchantable timber at a quicker rate when compared to wildfire in most of our study sites. At the same time, CWD was less abundant following timber harvest.

Such tradeoffs were more pronounced when considering indicators of wildlife habitat. Timber harvest promoted the growth of essential forage for moose, but it also resulted in forage for bears, a known predator of moose and caribou calves (Ballard 1992; Leblond et al. 2016; McLaren et al. 2021). Our results also demonstrated that even 31–40 years post-harvest, ample forage for both moose and bears was still available in cutblocks, whereas a preferred food source for caribou, terrestrial lichens, was still limited. These results were consistent across most of the ecosystems we sampled (i.e., central mixedwood, lower and upper boreal highlands).

Conclusions

We collected a large and geographically extensive set of field data and compared the temporal responses of multiple ecological indicators to timber harvest and wildfire. The differences in effect of these two disturbance types depends on the ecological attribute (e.g., timber volume, CWD, wildlife forage) and ecosystem subtype, and likely will be influenced by the size and severity of disturbance, pre-disturbance conditions, and silvicultural treatments (DeLong and Tanner 1996; Bergeron et al. 2004; Thiffault et al. 2007). Appropriate management will need to clearly establish which ecosystem attributes are a priority (e.g., wildlife conservation versus timber production), as a “one size fits all” solution is likely not feasible. Trade-offs may be necessary to maximize the functions and services provided by these ecosystems at a landscape scale. Our results suggest that wildfire is better at supporting the retention and supply of CWD and caribou forage. In contrast, timber harvest and associated activities lead to more rapid tree growth and supply of timber products. Therefore, timber harvesting and silviculture that better emulates wildfire, via retention of CWD, may improve the provisioning of the range of ecological indicators that we studied. Such an approach would be more aligned with EBM and could help maintain habitat for a range of species across the landscape.

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Author contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by all authors. The first draft of the manuscript was written and prepared by INB and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interest The authors declare no competing interests.

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