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Habitat loss accelerates for the endangered woodland caribou in western Canada

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Abstract

Habitat loss is often the ultimate cause of species endangerment and is also a leading factor inhibiting species recovery. For this reason, species-at-risk legislation, policies and plans typically focus on habitat conservation and restoration as mechanisms for recovery. To assess the effectiveness of these instruments in decelerating habitat loss, we evaluated spatiotemporal habitat changes for an iconic endangered species, woodland caribou (*Rangifer tarandus caribou*). We quantified changes in forest cover, a key proxy of caribou habitat, for all caribou subpopulations in Alberta and British Columbia, Canada. Despite efforts under federal and provincial recovery plans, and requirements listed under Canada's Species at Risk Act, caribou subpopulations lost twice as much habitat as they gained during a 12-year period (2000–2012). Drivers of habitat loss varied by ecotype, with Boreal and Northern Mountain caribou affected most by forest fire and Southern Mountain caribou affected more by forest harvest. Our case study emphasizes critical gaps between recovery planning and habitat management actions, which are a core expectation under most species-at-risk legislation. Loss of caribou habitat from 2000 to 2018 has accelerated. Linear features within caribou ranges have also increased over time, particularly seismic lines within Boreal caribou ranges, and we estimated that only 5% of seismic lines have functionally regenerated. Our findings support the idea that short-term recovery actions such as predator reductions and translocations will likely just delay caribou extinction in the absence of well-considered habitat management. Given the magnitude of ongoing habitat change, it is clear that unless the cumulative impacts of land-uses are effectively addressed through planning and management actions that consider anthropogenic and natural disturbances, we will fail to achieve self-sustaining woodland caribou populations across much of North America.

Dale Seip is retired.

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KEYWORDS

habitat loss, endangered species, species at risk, woodland caribou

1 | INTRODUCTION

Worldwide, more than 5,000 vertebrate species are at risk of extinction (IUCN, 2020a). The primary threats to terrestrial species are habitat loss and alteration, overexploitation, and the spread of invasive species (Maxwell, Fuller, Brooks, & Watson, 2016; Young, McCauley, Galetti, & Dirzo, 2016). Habitat loss, which can be defined as the permanent or temporary conversion of favorable habitat to an altered state, is a strong predictor of species endangerment (Kerr & Cihlar, 2004) and is a primary justification for listing species as endangered (Venter et al., 2006; Woo-Durand et al., 2020). Because habitat loss is also a leading factor inhibiting the recovery of endangered species (Kerr & Deguise, 2004), North American species-at-risk legislation such as Canada's *Species at Risk Act* and the United States' *Endangered Species Act* focus on concepts related to habitat conservation and restoration to promote species persistence and recovery (Taylor, Suckling, & Rachlinski, 2005; Adamowicz, 2016; Government of Canada, 2020).

With roughly 177 km^2 of natural lands being altered daily in the world and global habitat loss rates dramatically increasing (Theobald, Kennedy, Oakleaf, & Baruch-Mordo, 2020), species protection and recovery will depend on the identification of areas undergoing habitat change and of priority areas for conservation or restoration (Bruggeman, Jones, Lupi, & Scribner, 2005; Huxel & Hastings, 1999). Likewise, an analysis of the effectiveness of current recovery plans to conserve and restore habitat is fundamental to understanding why only a few species at risk of extinction have fully recovered and most continue to decline (Favaro et al., 2014; IUCN, 2020a; Taylor et al., 2005).

Here we evaluate the direction and extent of habitat change within the ranges of an iconic species at risk, woodland caribou (*Rangifer tarandus caribou*) to assess the effectiveness of existing recovery policies and plans at conserving habitat. Woodland caribou are a priority species for recovery efforts under the *Species at Risk Act* (SARA) in Canada, where various populations are considered as Threatened, Endangered, or of Special Concern (COSEWIC, 2014; Government of Canada, 2020). Yet most populations continue to decline across Canada (Festa-Bianchet, Ray, Boutin, Côté, & Gunn, 2011; Fryxell et al., 2020; Hervieux et al., 2013), despite recovery strategies and plans, and the cultural, social, and ecological significance of this species (Hummel & Ray, 2008). In the United States, woodland caribou were listed as endangered under the *Endangered Species Act* in 2019 (Fish and Wildlife Service, 2019), the same year they became extirpated from the lower 48 states (Serrouya et al., 2019). Woodland caribou are distributed over areas that face one of the most rapid rates of land-use change in the world (Hansen et al., 2013).

The primary threat to woodland caribou populations is broad-scale human-caused change to landscapes (Festa-Bianchet et al., 2011; Johnson et al., 2020; Latham, Latham, McCutchen, & Boutin, 2011), which compromises overall environmental conditions for caribou by directly disrupting landscape characteristics and associated predator–prey systems. More specifically, habitat change from forest fires and many aspects of industrial natural resource extraction shifts caribou habitats toward early-seral forests that are not suitable caribou habitats. This conversion of mature and old forests into early-seral forests also favors other ungulate species (Wittmer, McLellan, Serrouya, & Apps, 2007) and leads to increased predation on caribou via apparent competition (Festa-Bianchet et al., 2011; Latham et al., 2011; Serrouya et al., 2021). Increased predation pressure on caribou resulting from early-seral forests is exacerbated by the creation of linear features (e.g., roads, pipelines, transmission lines, and seismic lines), which alters the functional response of predators (Apps et al., 2013; DeMars & Boutin, 2018; Dickie, Serrouya, McNay, & Boutin, 2017; Mumma, Gillingham, Parker, Johnson, & Watters, 2018; Whittington et al., 2011). Habitat loss within caribou ranges can reduce caribou recruitment (Johnson et al., 2020), occupancy and range size (e.g., Vors, Schaefer, Pond, Rodgers, & Patterson, 2007), as well as increase adult caribou mortality (Fryxell et al., 2020; McLoughlin, Dzus, Wynes, & Boutin, 2003; Wittmer et al., 2007). Significant challenges are associated with conserving and recovering woodland caribou, particularly in relation to the many natural resources found within caribou ranges, and the associated employment and economic benefits that society derives from the exploitation of these natural resources (Hebblewhite, 2017).

Federal recovery goals for woodland caribou include achievement of self-sustaining populations across all their range, which necessitates long-term conservation and restoration of habitat (Environment Canada, , 2012b, 2014). SARA requires the development of action plans, which must outline how critical habitat conservation and recovery will be achieved through time. Critical habitat for woodland caribou has been defined as the habitat containing biophysical attributes required by caribou to

carry out life processes and limits on cumulative disturbance within population ranges (Environment Canada, 2014). In addition to this acknowledged importance of habitat management, recovery actions related to the proximal causes of caribou declines (apparent competition) have been increasingly taken to avoid extirpation of specific local populations (Environment Canada, 2014; Festa-Bianchet et al., 2011). Direct predator and prey reductions can be effective in the short-term (Hervieux, Hebblewhite, Stepnisky, Bacon, & Boutin, 2014; Serrouya et al., 2019; Serrouya, McLellan, van Oort, Mowat, & Boutin, 2017) but are controversial (e.g., Hervieux, Hebblewhite, Stepnisky, Bacon, & Boutin, 2015) and are intended to be temporary stop-gap measures while habitat recovers. This reasoning leads to the inevitable question: how long will predator and prey management need to take place until habitat can once again support caribou populations? The answer will be highly dependent on the direction and pace of ongoing habitat change, which in turn may be affected by policy instruments and recovery actions.

In our spatiotemporal analyses, we evaluate whether changes in forest cover (hereafter termed caribou habitat) within woodland caribou ranges are on a trend to meet recovery goals and objectives. We specifically tested whether caribou habitat loss shows a decreasing trend over time. Because woodland caribou require large contiguous areas of mature and old forests (Apps et al., 2013; Apps, McLellan, Kinley, & Flaa, 2001; Wittmer et al., 2007), we used changes in forest cover as a proxy of changes in caribou habitat. We also quantified the rate of linear feature creation across caribou ranges, and in a subanalysis where data were available, we evaluated the proportion of linear features that demonstrated vegetation recovery to a height that was found to slow wolf movement (Dickie et al., 2017), which could help mitigate some effects of linear features on facilitated predation.

2 | METHODS

2.1 | Study area and study species

We evaluated caribou habitat change within all woodland caribou ranges identified in Alberta (AB) and British Columbia (BC), which includes some of the most endangered caribou populations in Canada (Figure 1). Our study includes all three western woodland caribou ecotypes identified in federal recovery strategies and management plans: Boreal, Southern Mountain, and Northern Mountain, including all three groups of Southern Mountain caribou (southern group, central group, and northern group; Environment Canada, 2012b, 2014; Figure 1). All three ecotypes have been listed in the *Species at Risk Act* (SARA); Boreal and Southern Mountain caribou are considered Threatened, whereas Northern Mountain caribou are considered a population of Special Concern (Government of Canada, 2020). These ecotypes correspond to portions of Designable Units 6 through 9 (Boreal, Northern Mountain, Central Mountain, and Southern Mountain, respectively, which were defined to facilitate status assessment for all caribou in Canada; COSEWIC, 2011). In 2014, the central and southern groups were assessed as Endangered because of continued population declines (COSEWIC, 2014) but the Species At Risk Registry has not been amended by the federal government in accordance with the assessment.

We used provincial maps to delimit caribou subpopulation range boundaries (AB: https://extranet.gov.ab.ca/srd/geodiscover/srd_pub/LAT/FWDSensitivity/CaribouRange.zip; BC: https://catalogue.data.gov.bc.ca/dataset/caribou-herd-locations-for-bc—updated with data provided by the BC Government) and federal recovery strategies and management plans (Environment Canada, 2012b, 2014) to classify caribou ecotypes and groups.

2.2 | Policy instruments

Woodland caribou conservation and management in Canada is guided by federal and provincial policies, recovery strategies and management plans, all of which are heavily based on principles of habitat conservation and restoration. For instance, SARA legally protects critical habitat identified in recovery strategies of listed species (Canada, 2002) and the federal recovery strategies for Boreal and Southern Mountain caribou (released in 2012 and 2014, respectively) outline recovery objectives to minimize and mitigate alteration of critical habitat (Environment Canada, 2014), while the federal management plan for Northern Mountain caribou (released in 2012) set out management goals and objectives for this ecotype (Environment Canada, 2012b). Neither AB nor BC has provincial species-at-risk legislation so caribou protection relies on federal statutory rules and existing provincial laws and policies (Palm, Fluker, Nesbitt, Jacob, & Hebblewhite, 2020).

2.3 | Measuring changes in habitat within caribou ranges

2.3.1 | Forest cover

We derived forest cover change information from Landsat imagery at 30-m resolution (i.e., 1:120,000 scale).

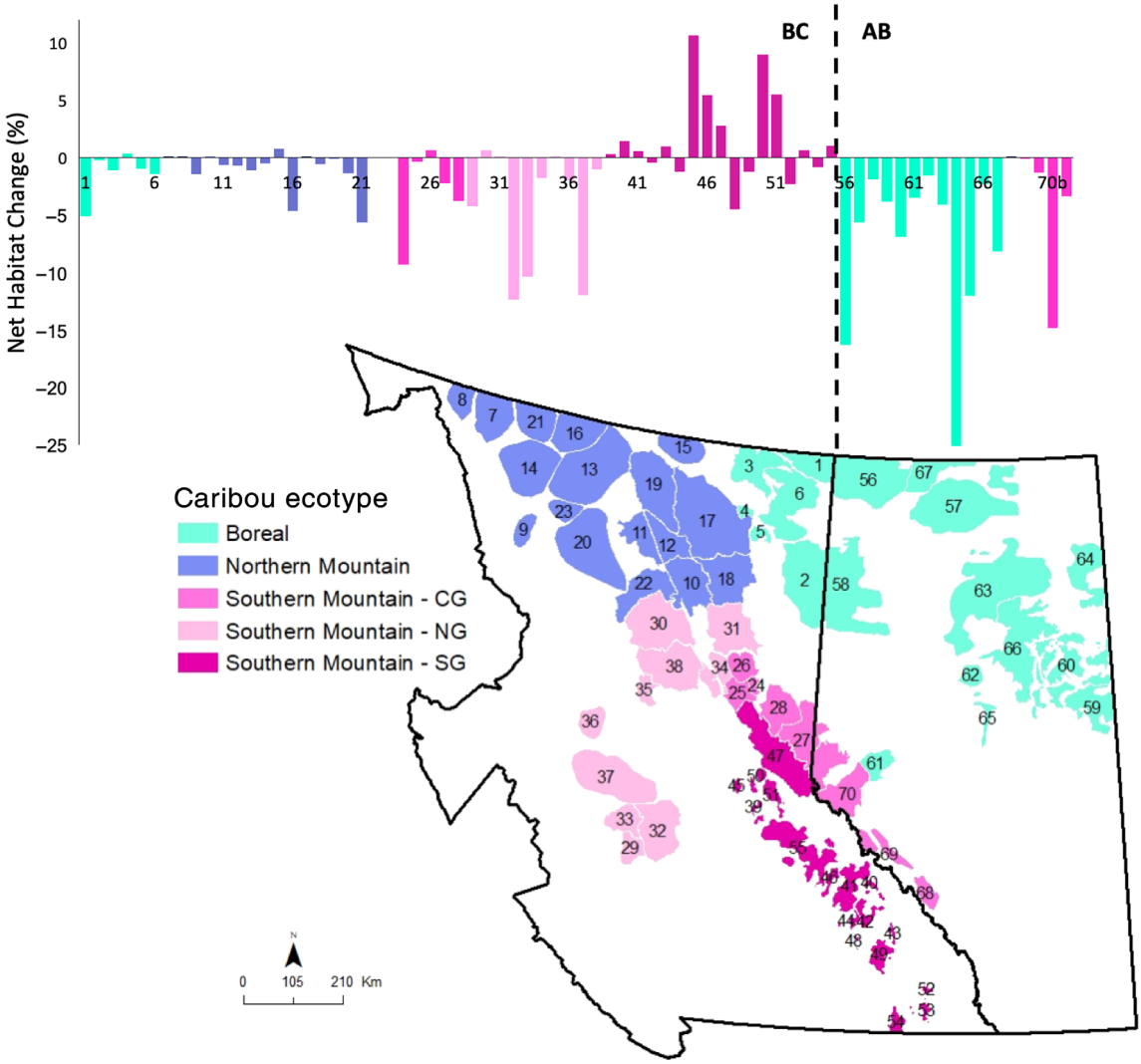

FIGURE 1 Net change of caribou habitat (measured as forest cover) in Alberta (AB) and British Columbia (BC) from 2000 to 2012. Net habitat change (%) = forest cover gain within caribou range (%) minus forest cover loss (%). Positive forest cover change values represent net gain and negative values represent net loss. Bars represent individual caribou ranges each identified with a number (Appendix S5). CG, central group; NG, northern group; SC, southern group

Remotely sensed data on changes in forest cover were obtained from the Global Forest Change (GFC) dataset (methods described in Hansen et al., 2013). The GFC assessed annual forest loss by comparing conditions from 1 year to the subsequent year from 2000 through 2018 (e.g., "2017–2018 loss" represents loss observed from comparing 2017 forest cover to that of 2018). In this dataset, forest cover loss was defined as a stand-replacement disturbance, or the complete removal of tree canopy (Hansen et al., 2013). Forest cover gain, which was defined by GFC as the inverse of loss, or the return of tree canopy, was quantified for the period 2000–2012 by comparing forest cover in 2012 to that of 2000 (Hansen et al., 2013). We identified sources of forest loss by stratifying the forest loss pixels from the GFC using the Canada Landsat Disturbance dataset, which contains annual data on forest fire and forest harvest up to 2015 (CanLaD; Guindon et al., 2017). We classified forest cover loss pixels not identified by CanLaD as originating from either fire or harvest as "other losses," which represents canopy loss from other sources, including insect outbreaks (Guindon et al., 2018).

We used changes in forest cover as a proxy for changes in caribou habitat because woodland caribou require large contiguous areas of mature and old forests (Apps et al., 2001; Apps et al., 2013; Wittmer et al., 2007). We used forest cover gain to quantify forest regeneration and used this metric as an index representing the transition out of the early-seral forest stage that benefits competing ungulates, to help inform whether habitat conditions are on trend to meet caribou requirements. To account for differences in caribou range sizes, all habitat

metrics (loss, gain, forest fire, forest harvest, and "other losses") were calculated as a percentage (0–100%) within each caribou subpopulation range (i.e., cumulative values for each range at the end of the study period divided by the range size). We expressed the habitat metrics as annual values by dividing cumulative values (loss, gain, forest fire, harvest, and "other losses") within each caribou range (%) by the number of years in which data were collected. We calculated net habitat change for the entire 2000–2012 period by subtracting cumulative forest loss (%) within individual ranges from their respective cumulative forest gain (%). Positive habitat change values represent net gain (i.e., more gain than loss) and negative values represent net loss (i.e., more loss than gain; see Appendix S1 for equations used to estimate habitat metrics).

Gross forest cover gain estimates, such those as used in this study, may be conservative because forest gain is not as easily detected as forest loss, especially in low-productivity boreal forests (Guindon et al., 2018). On the other hand, this gain metric assumes the forest is returning after 5 m of growth (Hansen et al., 2013), which, in most ecological settings, does not represent full recovery of caribou habitat. This structural stage may approximate the period when forage (i.e., shrubs) for competing ungulates dissipates (Wittmer et al., 2007; see Appendix S2), but typically does not represent lichen-bearing forage habitat for caribou (Proceviat, Mallory, & Rettie, 2001; Stevenson et al., 2001). We note that management actions taken during the study period could not have resulted in 5 m of forest growth in the ecological settings of most caribou ranges; however, estimates of negative net changes in forest cover (caribou habitat) remain indicative of forest loss exceeding recruitment of new forest during the study period.

We conducted a two-way analysis of variance (ANOVA) for unbalanced designs with individual ranges as the experimental unit to compare caribou forest change metrics (loss, gain, forest fire, harvest, and net change) across caribou ecotypes (Boreal, Northern Mountain, and Southern Mountain—southern group, central group, northern group) and provinces where ranges are located (AB and BC). Interactions between ecotype and province were also considered.

We compared the gross area of forest cover loss in recent years (2009–2018) with previous years (2000–2008) using a *t*-test with year as the experimental unit to evaluate whether caribou habitat loss has decelerated during the last decade. We then assessed whether the federal recovery strategy/management plan for each ecotype is associated with a decrease in habitat loss within their ranges by comparing the annual gross area of habitat loss before (Boreal and Northern Mountain caribou: 2000–2012; Southern Mountain caribou: 2000–2014) and after (Boreal and Northern Mountain caribou: 2013–2018; Southern Mountain caribou: 2015–2018) its release using a Welch approximation t-test, which is designed for unbalanced designs. Our prediction was that caribou habitat loss would decrease after the release of such policy instruments, particularly within the ranges of caribou ecotypes listed as Threatened (i.e., Boreal and Southern Mountain caribou).

We applied a centered log-ratio transformation to any proportional data to break data circularity and checked whether data met test assumptions prior to conducting statistical analysis. We performed all statistical analyses in R software (R Development Core Team, 2019) with the packages compositions (Boogaart, Tolosana-Delgado, & Bren, 2021) and car (Fox et al., 2020).

2.3.2 | Linear features

Linear features negatively affect woodland caribou by increasing the occurrence of early seral vegetation, and by facilitating predator hunting efficiency and encroachment into caribou habitat (Apps et al., 2013; DeMars & Boutin, 2018; Dickie et al., 2017; Mumma et al., 2018). Because we quantified forest-cover loss using 30-m imagery (GFC), linear features that are typically 8-m wide or less are not well captured. Therefore, we quantified the length and density of linear features (LFs) within caribou ranges in AB and BC using vector datasets with visually identified LFs (AB: 2010–2018, BC: 1996–2018; see Appendix S3 for details on datasets) as a separate analysis to quantify the rate of LF creation. We calculated the annual rate of LF creation in each province by subtracting either the length (km) or density of LF (m/km^2) in year t from values in year $t + 1$.

We then estimated the rate of natural vegetation regrowth on seismic lines to quantify regeneration rates. We estimated the rate of regrowth for AB only, which had near-complete coverage of Light Detection and Ranging (LiDar) data, with the exception of Bistcho, Caribou Mountains, and Yates caribou ranges (see Appendix S4), which were excluded from the natural-regeneration analysis. LiDar data were not available in BC because of patchy coverage and data-use restrictions from privately owned data. We first quantified vegetation height on seismic lines using Least Cost Paths (LCPs) created between intersections of seismic lines with other features (see Appendix S4 for details on LCP analysis and provincial LiDar data). We then measured the rate (in m/yr) of vegetation regrowth from the year in which the seismic lines were cut (i.e., time since cut; ABMI, 2018) to the year in which vegetation height was measured. For seismic line

segments where LiDar data were not available, such as those that were created after LiDar data acquisition, we estimated the vegetation height along the LCP using the median growth rate based on the dominant ecosite for that LCP. Ecosite characteristics have previously been shown to influence vegetation regrowth on seismic lines (van Rensen et al., 2015; see Appendix S4 for additional details). An important assumption of our approach is that all seismic lines with similar ecosite characteristics regenerate at equal rates.

Finally, we compared the rate of linear feature creation to the percent length and density of seismic lines that were naturally regenerating. Vegetation heights of 0.5, 0.7, and 4.1 m have been respectively associated with reductions of wolf travel speed on seismic lines (Dickie et al., 2017; Finnegan et al., 2018). These estimates could therefore help to inform when LFs are functionally regenerated in the context of caribou recovery (i.e., when vegetation has sufficiently regenerated to no longer benefit predator movement along LFs). Here we adopted the lower (0.5 m) and upper (4.1 m) values as proxies of partial and full functional regeneration thresholds for vegetation height on seismic lines (Dickie et al., 2017) but we highlight that, in many forest types, ecological recovery of caribou habitat on linear features would require more than 0.5 and 4.1 m of forest regrowth. We calibrated the vegetation height values from a province-wide LiDar dataset to values from the LiDar dataset used by Dickie et al. (2017) to extrapolate findings to the rest of the province. We identified that these two thresholds represented 0.92 m (partial regeneration) and 6.67 m (full regeneration) in the provincial-wide LiDar dataset (see Appendix S4 for details on calibration methods). We calculated the annual and cumulative percent length and density of seismic lines that met each regeneration threshold for each caribou range. We then summarized the cumulative percent length and density of seismic lines that were identified as regenerated for each caribou range, as well as the mean annual regeneration rates to compare against linear feature creation.

Mean values for length and density across ranges were weighted by range sizes. We performed all spatial analyses in ArcGIS software (ESRI, 2009).

3 | RESULTS

3.1 | Forest cover

From 2000 to 2018, at least 33,140 km^2 of caribou habitat (measured as forest cover) were lost in AB and BC (annual loss area: mean = 1,841 km^2 [SD 993]; Figure 2). Habitat loss had an increasing trend over time (Figure 2) and accelerated during the latter decade (annual forest loss area 2000–2008: mean = 1,366 km^2 (SD 566; annual forest loss area 2009–2018: mean = 2,316 km^2 (SD 1,125); $t_{(11.8)} = -2.26$, $p < .05$). At least seven caribou ranges have lost nearly a quarter of their habitat from 2000 to 2018 (Figure 3) and annual habitat loss in AB was about twice that of BC (AB: mean = 0.60% (SD 0.41); BC: mean = 0.32% (SD 0.29)).

Overall, caribou habitat changes were contingent on an interaction between caribou ecotype and the province where ranges are located (Table 1; loss: $F_{(1,4)} = 6.598$, $p = .01$; gain: $F_{(1,4)} = 9.414$, $p < .01$; net change: $F_{(1,4)} = 4.716$, $p < .05$; forest harvest: $F_{(1,4)} = 7.836$, $p < .01$). Forest fire was a major source of habitat loss (Figure 2), regardless of caribou ecotype and province ($F_{(1,4)} = 1.470$, $p > .05$). Despite being highly variable across ranges, forest fire was the main source of loss in 78% of Boreal caribou ranges and 65% of Northern Mountain caribou ranges (Figure 3). Indeed, mean annual forest fire losses within the ranges of Boreal caribou in AB were at least three times greater than within the ranges of any other ecotype (Table 1). The annual forest harvest in both AB and BC, and other alterations such as insect outbreaks in BC, also represented an important source of habitat loss, particularly for Southern Mountain caribou (Figure 2; Table 1). Forest harvest alone was the main driver of loss within 1/4 of the ranges, most of which were Southern Mountain caribou (Figure 3). Forest harvest accounted for more than 70% of the habitat loss within three caribou ranges (Groundhog in BC, Narraway and Little Smoky in AB) and more than 30% in another 25 ranges, including Redrock-Prairie Creek and À La Pêche in AB, George Mountain, North Cariboo, Telkwa, Takla, Wolverine, and Scott in BC (Figure 3).

Overall, habitat loss has not decreased since the release of federal policy instruments for woodland caribou (Figure 2; Boreal caribou: $t_{(6.52)} = -0.50$, $p > .05$; Northern Mountain caribou: $t_{(4.38)} = -1.18$, $p > .05$; Southern Mountain caribou: $t_{(2.75)} = -0.37$, $p > .05$;). The mean annual loss after the release of the strategies/plans has increased up to 262% (Boreal caribou: mean before = 855 km^2 (SD 773), mean after = 1,081 km^2 (SD 881); Northern Mountain caribou: mean before = 140 km^2 (SD 146), mean after = 367 km^2 (SD 420); Southern Mountain caribou: mean before = 703 km^2 (SD 337), mean after = 787 km^2 (SD 361)).

With an overall annual habitat loss rate of over twice the gain (loss: mean = 0.39% (SD 0.34); gain: mean = 0.17% (SD 0.20)), habitat change within caribou ranges did not demonstrate achievement of no net loss (net change from 2000 to 2012: mean = −2.13% [SD −2.05]). For instance, from 2000 to 2012, loss exceeded gain in 58% of the caribou ranges (Figure 1; Appendix

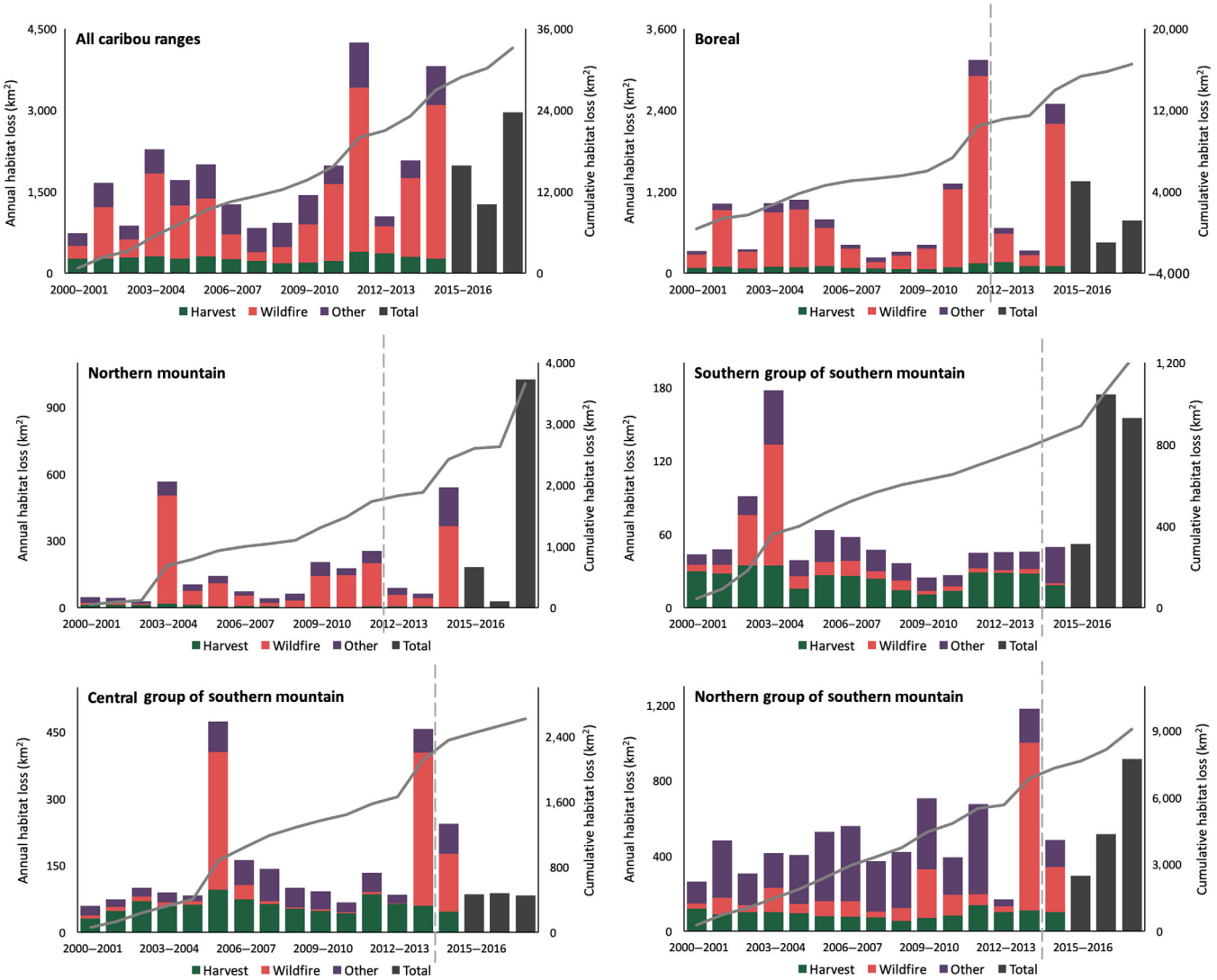

FIGURE 2 Gross annual loss of caribou habitat in Alberta and British Columbia, Canada. Habitat loss was measured as loss of forest cover captured by 30-m resolution imagery, which does not include linear features. Habitat loss was stratified by alteration type for years when data were available (prior to 2015). Dashed lines represent the release of the federal recovery strategy or management plan for each caribou ecotype. Cumulative habitat loss in solid gray line. Note differences in scale between panels

S5). In AB, none of the ranges experienced net habitat increase (i.e., more forest regeneration than loss), and gain offset loss (i.e., forest regeneration equal to loss) in only two ranges (Banff and Jasper; Figure 1; Appendix S5). The highest annual habitat loss and the poorest net change were within the ranges of Boreal caribou in AB (mean = 0.69% (SD 0.37) and −7.60% (SD 7.1), respectively), which were about three to five times higher than in BC (annual loss: mean = 0.27% (SD 0.19); net change: mean = −1.41% (SD 1.91)). Most net habitat gain (i.e., forest regeneration) occurred within the ranges of Southern Mountain caribou in BC, particularly within the ranges of the southern group, which was the only ecotype with positive net change (Figure 1; Table 1; Appendix S5).

3.2 | Linear features

The density of LFs within woodland caribou ranges has increased over time, particularly within Boreal ranges (Table 2; Figure 4). As of 2018, the extent of linear features within caribou ranges in AB and BC was 750,074 km (AB: 357,346.28 km; BC: 392,727 km), or a density of 2.38 km/km^2 and 1.20 km/km^2 in each province, respectively (Figure 4; see Appendix S6 for range-specific values). The vast majority of the LFs in these two provinces were seismic lines (AB: 79% of LFs, density = 1.73 km/km^2, SD 1.31; BC: 66%, density = 0.65 km/km^2, SD 1.47). The annual rate of creation varied from 18 m/km^2 in Chinchaga to a maximum of 309 m/km^2 in Cold Lake (Table 3).

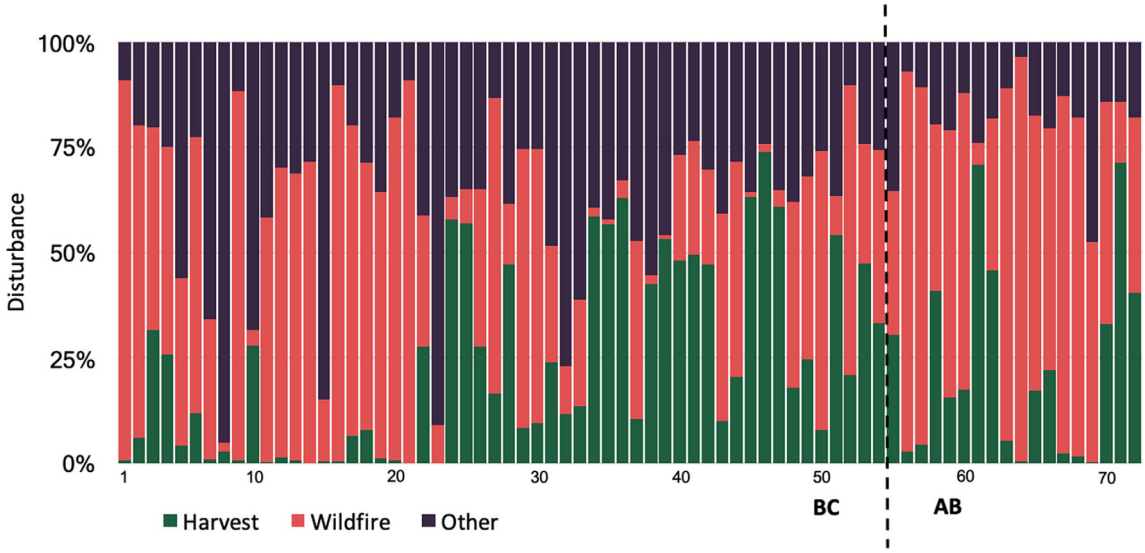

FIGURE 3 Percent disturbance from harvest, fire or other, making up habitat loss (as represented by forest cover change) within caribou ranges in Alberta (AB) and British Columbia (BC) from 2000 to 2015. Bars represent individual ranges of Boreal, Southern Mountain, and Northern Mountain caribou, each identified with a number (Appendix S4)

TABLE 1 Annual rate of habitat change (measured as forest cover; mean % and SD) within the ranges of five caribou ecotypes in Alberta (AB) and British Columbia (BC)

Province	Caribou ecotype	*N*	Loss	Gain	Net change	Harvest	Fire	Other losses
AB	Boreal	12	0.69 (0.37)	0.08 (0.10)	−7.60 (7.07)	0.11 (0.14)	0.52 (0.49)	0.09 (0.04)
AB	Southern Mountain—CG	5	0.40 (0.47)	0.09 (0.07)	−3.92 (6.23)	0.26 (0.44)	0.13 (0.08)	0.07 (0.08)
BC	Boreal	6	0.27 (0.19)	0.03 (0.02)	−1.41 (1.91)	0.02 (0.01)	0.16 (0.17)	0.08 (0.11)
BC	Northern Mountain	17	0.12 (0.13)	0.03 (0.03)	−1.05 (1.828)	<0.01 (0.01)	0.08 (0.10)	0.03 (0.02)
BC	Southern Mountain—SG	17	0.26 (0.18)	0.35 (0.29)	1.61 (3.95)	0.09 (0.10)	0.06 (0.06)	0.07 (0.07)
BC	Southern Mountain—CG	5	0.58 (0.29)	0.26 (0.12)	−3.00 (3.89)	0.25 (0.21)	0.15 (0.14)	0.19 (0.13)
BC	Southern Mountain—NG	10	0.65 (0.36)	0.27 (0.12)	−4.28 (5.22)	0.16 (0.11)	0.16 (0.18)	0.31 (0.26)

Notes: All values refer to annual estimates, except net change, which is for the entire period of 2000–2012. Net habitat change (%) = forest cover gain within caribou range (%) minus forest cover loss (%). Positive habitat change values represent net gain and negative values represent net loss.
Abbreviations: CG, central group; N, number of caribou ranges analyzed; NG, northern group; SG, southern group.

TABLE 2 Annual rate of creation of all linear features (LFs) and seismic lines within caribou ranges in Alberta (AB) and British Columbia (BC)

		All LFs		Seismic lines only	
Province	Ecotype	Length (km)	Density (m/km^2)	Length (km)	Density (m/km^2)
AB	B	543 (1,435)	62 (172)	454 (1,409)	51 (166)
AB	SM	39 (107)	3 (9)	11 (29)	1 (2)
BC	B	1,254 (2,787)	153 (278)	956 (2533)	115 (255)
BC	NM	96 (384)	9 (36)	50 (311)	4 (29)
BC	SM	184 (668)	483 (149)	68 (488)	13 (88)

Notes: Mean rate and standard deviation (in brackets) were measured as annual increase in LF (values in year $t + 1$ – values in year t).
Abbreviations: AB data, 2010–2018; B, Boreal caribou; BC data, 1996–2018; NM, Northern Mountain caribou; SM, Southern Mountain caribou.

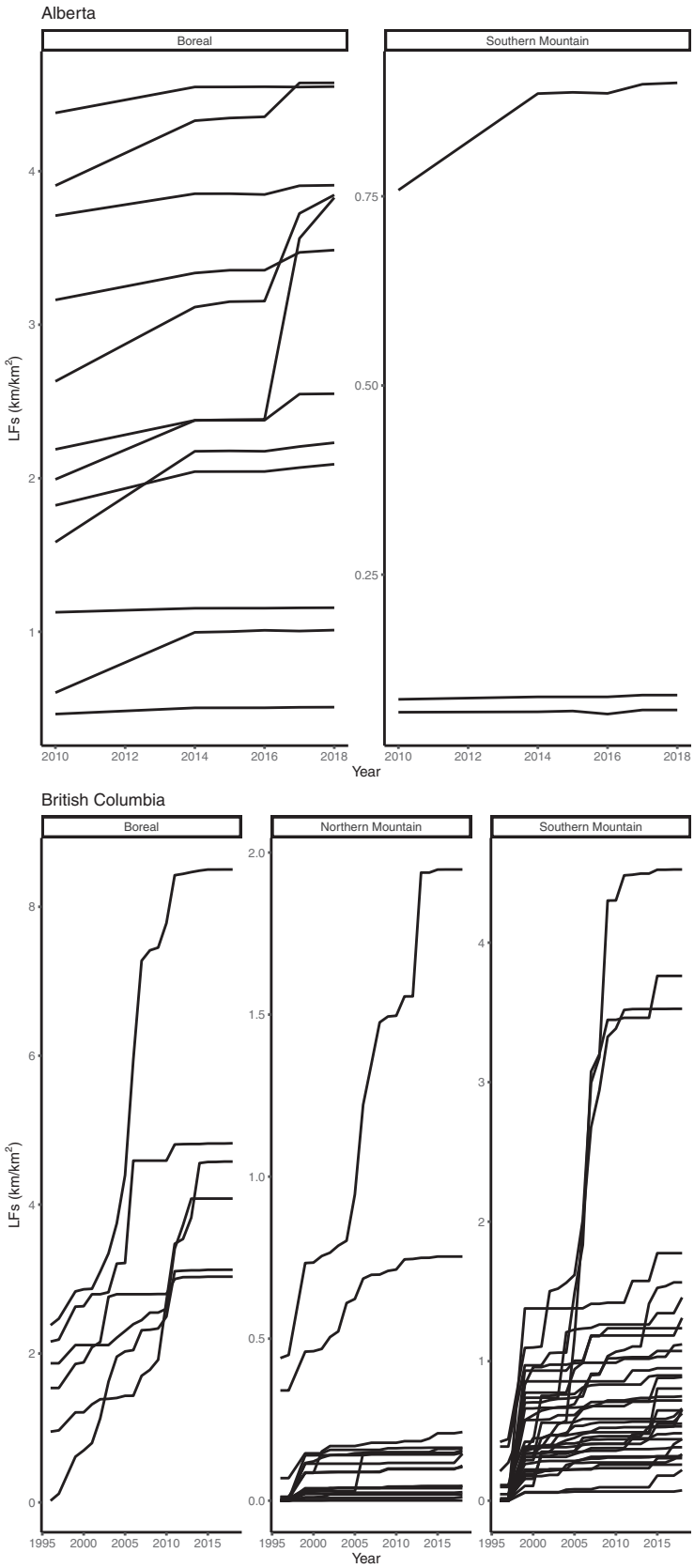

FIGURE 4 Density of linear features (LF) within caribou ranges in Alberta (2010–2018) and British Columbia (1996–2018). Lines represent individual caribou ranges

On average, as of 2018, 59% of the linear features across AB's caribou ranges (in which LiDar data were available) had recovered to the 0.92-m partial-regeneration threshold. Only a mean of 5% (range = 1–10%) of linear features had met the full regeneration threshold of 6.67 m. When accounting for the rate of natural

TABLE 3 Mean annual rate of linear feature (LF) creation, regeneration of LFs, and net LF change in length (km) and density (km/km^2) in boreal caribou ranges in Alberta from 2010–2018

	LF length (km)					LF density (m/km^2)						
		Regeneration rate/yr		Net change/yr			Regeneration rate/yr		Net change/yr		Regenerated (%)	
Range	Creation rate/yr	Partial	Full	Partial	Full	Creation rate/yr	Partial	Full	Partial	Full	Partial	Full
Chinchaga	321	822	524	502	203	18	47	30	28	12	80	7
Cold Lake	2,080	1,138	104	−942	−1,976	309	169	15	−140	−294	48	3
East Side Athabasca	2,234	1,271	164	−963	−2,069	170	97	12	−73	−158	36	2
Little Smoky	217	161	104	−57	−113	70	52	34	−18	−37	89	9
Nipisi	93	83	39	−10	−54	44	39	19	−45	−26	66	10
Red Earth	509	639	392	130	−117	21	26	16	5	−5	52	6
Richardson	159	142	6	−17	−154	22	20	1	−2	−22	52	1
Slave Lake	59	81	14	23	−44	39	53	9	15	−29	62	6
West Side Athabasca	640	533	135	−107	−505	41	34	9	−7	−32	48	4
Mean	701	541	165	−160	−537	82	60	16	−22	−66	59	5

Notes: The percent length of seismic lines that were estimated to have met partial and full regeneration targets as of 2018 are also provided for each caribou range (regenerated (%)). Regeneration was defined using both a partial recovery threshold (0.92 m) and full recovery threshold (6.67 m). Net LF change = LF regeneration within caribou range minus LF creation. Positive net rate values represent net gain (LF regeneration) and negative values represent net loss (LF creation). Mean values were weighted by range area.

regeneration to the partial or full regeneration targets, the net change in LF averaged −22 m/km^2 and −66 m/km^2, respectively, which means that the LF creation rate outpaces the LF regeneration rate. From 2010 to 2018 in Alberta, only three caribou ranges out of nine had lower LF creation rates than regeneration rates to the partial regeneration target and only one of them had lower creation rates than regeneration rate to the full regeneration target (Table 3).

4 | DISCUSSION

Habitat loss is the greatest driver of species endangerment in Canada (Venter et al., 2006; Woo-Durand et al., 2020), and long-term habitat conservation and restoration across broad areas will be necessary to recover most of Canada's endangered species (Kerr & Deguise, 2004), including woodland caribou (Environment Canada, 2014; Johnson et al., 2020). Spatial information that quantifies habitat change can improve a species' chance of recovery, if that information is used to prioritize areas for conservation and restoration (Huxel & Hastings, 1999). For caribou, range-level information can be used to identify priority areas for conservation and recovery actions. Areas with high habitat alteration (i.e., of high risk to caribou) should be targeted with interventions to both decrease habitat alteration and to restore lost habitat. Because habitat recovery (either natural or through restoration efforts) entails large time lags (e.g., Curran, Hellweg, & Beck, 2014; Lee & Boutin, 2006), our spatial analysis also helps frame targeted proximate recovery actions such as predator reductions. In areas where forest loss exceeds gain, which is 60% of the ranges reported here, the implication is that predator reductions merely delay caribou extinction if new habitat alterations are not addressed and lost habitat is not restored.

Our analysis on forest cover changes presents an alarming picture of continuing habitat loss within caribou ranges, despite provisions listed in SARA and federal and provincial recovery strategies or plans. That said, it would be unrealistic to expect immediate results after the release of such policy instruments, particularly results related to forest regeneration, which entails large time lags (e.g., Curran et al., 2014; Lee & Boutin, 2006). However, with habitat loss increasing over time, our results reveal that there has not been much evident progress toward conserving caribou habitat in AB and BC, even 6–8 years after the release of the federal recovery strategies or management plans. Habitat loss increased up to 262% after the release of these federal policy instruments. The Itcha-Ilgachuz range in BC, for example, has lost 2,120 km^2 of forest cover and experienced an associated dramatic caribou population decline of 90% since 2000 (BC Government data files, C. Shores BC Government Ministry). The one exception may be the southern group of Southern Mountain caribou, where the provincial recovery process (MCRIP, 2007) resulted in the protection of 22,000 km^2, of which ∼20% is potentially harvestable (equivalent to the IUCN Protected Area Category IV; IUCN, 2020b). In these caribou ranges, gain offset the losses up to 2012. We cannot definitely conclude that the MCRIP (2007) process led to habitat gain exceeding loss during that time period because changing lumber prices leading to reduced harvesting could confound this interpretation. However, one would expect these changing prices to have affected net habitat change in all caribou ranges equally, whereas the net gain coincided with the area where MCRIP (2007) was implemented. In any case, we reemphasize that "gain" is essentially a transition out of early seral forest condition (Hansen et al., 2013), not complete gain of mature canopies that represent caribou foraging habitat. In the case of the southern group, the stated goal of stabilizing population declines by 2014 has not been achieved, nor has the goal of protecting "100% of the high suitability winter habitat" (MCRIP, 2007) due to the continued loss of habitat in some ranges.

The ability to enact meaningful habitat management measures in Canada typically depends upon policy instruments not primarily focused on species at risk because most wildlife is distributed over areas outside federal legislative powers (Fluker & Stacey, 2012; Palm et al., 2020). Our results support previous suggestions that despite adoption of species at risk listing representing a decision to regulate and manage, "legislative commitment to recovery planning does not necessarily mean a commitment to plan implementation" (Farrier, Whelan, & Mooney, 2007). Although implementation of recovery plans has generally been faulty in North America (Taylor et al., 2005; Farrier et al., 2007), the designation of critical habitat seems to improve species population trends in the United States (Taylor et al., 2005). Our findings reiterate the idea that, to the extent that they have jurisdiction, Canada's environmental assessment regimes are ineffective in protecting caribou habitat, whether it be formally designated critical habitat or otherwise (Collard, Dempsey, & Holmberg, 2020; Palm et al., 2020). Our case study emphasizes critical gaps between listing, recovery planning, and delivery of management actions related to habitat conservation and restoration. These gaps may shed light on why recovery planning has not been effective in recovering species at risk of extinction or improving their listing status (Bottrill et al., 2011) and why at-risk species

in Canada have rarely demonstrated recovery (Favaro et al., 2014).

Habitat change within caribou ranges also reflects ecoregion processes. Forest fire was the major source of habitat loss within most caribou ranges, particularly for the Boreal and Northern Mountain caribou that occur within ecosystems regulated by dynamic fire events (Brandt, Flannigan, Maynard, Thompson, & Volney, 2013). Forest fire reduces habitat availability for caribou and can indirectly increase predation by altering predator–prey dynamics and spatial use (Robinson et al., 2012; but see DeMars et al., 2019). The negative effects of forest fire on caribou recruitment, however, are three to four times lower in magnitude than human-related habitat alterations (Johnson et al., 2020). Historically, caribou have persisted in fire-dominated ecosystems by expanding their home ranges and shifting their habitat in response to forest fires (Courtois, Ouellet, Breton, Gingras, & Dussault, 2007). Now, however, the combined effects of dynamic fire regimes (Brandt et al., 2013), linear features that allow predators to encroach in refugia (DeMars & Boutin, 2018), and increased forest harvest, have contributed to broad-scale declines of boreal caribou (e.g., Hervieux et al., 2013; Stewart et al., 2020). Notwithstanding the fact that humans often initiate forest fires (Tymstra, Stocks, Cai, & Flannigan, 2020), subsequent management of large forest fires is difficult (Werth et al., 2011; Tymstra et al., 2020). Additional challenges include interactions with climate change, which is expected to increase the frequency and extent of fires in boreal forest (Price et al., 2013). Together with the proliferation of human-caused habitat alteration, climate change may also be contributing to the expansion of white-tailed deer into boreal areas (Dawe & Boutin, 2016), which can further impact woodland caribou via apparent competition. Considering the high proportion of habitat loss due to forest fire reported here, human-caused habitat alteration can be expected to exacerbate caribou declines (Johnson et al., 2020), which highlights the need to explicitly incorporate the complexity and unpredictability of natural disturbances into recovery planning.

We found that forest harvest was the primary source of forest cover loss for at least 1/4 of the caribou ranges, an important finding given that forestry can be managed and is a predictor of caribou mortality (Apps et al., 2013) and extirpation (Apps & McLellan, 2006; Vors et al., 2007). Forestry is the fastest-growing cause of land alteration in AB (ABMI, 2018). Although forest harvest most strongly affected Southern Mountain caribou ranges, it also affected Boreal caribou ranges in AB. For example, forest harvesting accounted for 70% of habitat loss in the Little Smoky range, where ongoing wolf population reductions have been used to help stem caribou extirpation (Hervieux et al., 2014).

Complex synergistic interactions between habitat alterations have been previously observed for caribou (Beauchesne, Jaeger, & St-Laurent, 2014) and other boreal species (Mahon, Holloway, Bayne, & Toms, 2019). Therefore, cumulative effects need to be considered when setting thresholds for human-related alterations and setting temporal and spatial objectives for species recovery. In western Canada, most common human-related alterations within caribou ranges include forest harvesting and linear features (e.g., seismic lines, roads). Forestry footprint has doubled in the last decade in AB (ABMI, 2018), and we found that linear features have also increased over time in AB and BC, with the rate of creation outweighing regeneration. The slow rate of natural vegetation regrowth is consistent with previous findings of stagnated succession in these systems (Lee & Boutin, 2006; van Rensen et al., 2015). The removal of trees, particularly in wet, low-productivity areas, can take centuries to recover, and forest regrowth on lines can be further compromised by continued recreational or industrial human-use (Lee & Boutin, 2006; van Rensen et al., 2015). In some caribou ranges, such as Cold Lake and East Side Athabasca, active habitat restoration treatments have been used to facilitate the return to tree cover (Dickie, McNay, Sutherland, Sherman, & Cody, 2021; Tattersall et al., 2019). For example, the Regional Industry Caribou Collaboration has conducted restoration treatments on over 1,200 km of linear features within East Side Athabasca and Cold Lake ranges since 2011, at an average of 136 km per year (Regional Industry Caribou Collaboration, unpublished data). Despite representing some of the largest-scale caribou habitat restoration programs to date, the net creation rate of linear features still exceeds 1,000 km per year in these ranges, even when habitat restoration is included. We note however that these two caribou ranges had particularly high creation rates, likely because of the expansion of dense low-impact seismic. Low-impact seismic are created differently than conventional seismic, and may have differential recovery rates (Charlebois, Skatter, Kansas, & Crouse, 2015). Given the negative impact of linear features on caribou (Apps et al., 2013; DeMars & Boutin, 2018; Dickie et al., 2017; Mumma et al., 2018), monitoring the net change in linear feature density across ranges is imperative for effective habitat management. While we present coarse metrics of creation and regeneration of linear features across AB, these metrics should be validated with field data and additional remote-sensing tools. The lack of updated and high-resolution vegetation monitoring data, such as those obtained using LiDar or other remote-sensing technology across caribou ranges in western Canada, is an

impediment to recovery planning and restoration-effectiveness monitoring.

Our results further support the idea that management practices such as predator reductions will simply delay eventual caribou extinction, unless effective habitat conservation, management, and recovery approaches are implemented (Festa-Bianchet et al., 2011). Given the current extent of habitat changes from human causes and forest fire within many woodland caribou ranges, predator reductions have been increasingly used to improve caribou survival and avoid their near-term extirpation (Potvin, Jolicoeur, Breton, & Lemieux, 1992; Hervieux et al., 2014; Serrouya et al., 2019). However, this action alone will not lead to self-sustaining caribou populations because the method does not address the ultimate causes of decline (Wittmer et al., 2007; Festa-Bianchet et al., 2011). In this sense, predator reductions are a palliative measure as caribou populations are prone to returning to decline soon after such actions cease (Johnson et al., 2019). Further, it is likely that effective predator management would become increasingly difficult, or impossible, as landscape alteration increases. Our study suggests that unless human-related habitat alterations are adequately addressed, the recovery of most woodland caribou populations seems unlikely.

We have known for decades that declines in woodland caribou populations are due to cumulative effects of natural and anthropogenic sources of habitat loss (Festa-Bianchet et al., 2011; Environment Canada, 2012b, 2014; Johnson et al., 2020). Our illustration of the trend and magnitude of caribou habitat loss supports the notion that if society wishes to act against woodland caribou declines, it needs to make long-term commitments to land-use planning and actions, including adequate reductions in habitat alterations from human sources and restoration of previously altered habitat (Festa-Bianchet et al., 2011). Unless we focus our efforts to address the ultimate cause of decline, we will fail to achieve self-sustaining woodland caribou populations.

Equations for habitat metrics (Appendix S1), age estimates for forest loss and gain (Appendix S2), linear feature datasets (Appendix S3), vegetation height on seismic lines (Appendix S4), and detailed range-level information on habitat change (Appendixes S5 and S6) are available online.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

AUTHOR CONTRIBUTIONS

Robert Serrouya and Dale Seip conceived the idea. Robert Serrouya, Mariana Nagy-Reis, Anna Calvert, Mark Hebblewhite, Dave Hervieux, Dale Seip, Sophie Gilbert, Oscar Venter, and Stan Boutin designed the project. Mariana Nagy-Reis collected and analyzed the data, interpreted the results, elaborated the tables and figures, and drafted the manuscript. Melanie Dickie and Sophie Gilbert assisted with linear feature analysis and tables. Robert Serrouya supervised the project. Melanie Dickie and Craig DeMars provided feedback and expertise on the linear feature analysis. All authors critically reviewed the manuscript, contributed to writing, and approved the submitted version.

ETHICS STATEMENT

This manuscript describes original work, has not been published, and is not under consideration for publication elsewhere.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on GitHub (https://github.com/MelanieDickie/HabitatGainAndLoss).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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