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Incorporating mechanism into conservation actions in an age of multiple and emerging threats: The case of boreal caribou

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Abstract

Conservation strategies for imperiled species are frequently based on identifying and addressing the probable causes of population decline, an approach known as the declining population paradigm. Causes, however, are frequently linked to demographic outcomes by multiple mechanisms, and failing to target the primary mechanisms can reduce the effectiveness and efficiency of conservation actions. Increasingly, conservation strategies also need to consider emerging threats, such as climate change. Here, we use boreal caribou (*Rangifer tarandus caribou*), a threatened ecotype of woodland caribou, as a case study to illustrate how landscape disturbance and climate change can each exert negative demographic effects on caribou through multiple and complex mechanisms. We reviewed the extensive literature focused on woodland caribou to identify and assess the relative importance of each putative mechanism. While disturbance-mediated apparent competition, the expansion of novel predators, and altered predator behavior appear to be primary mechanisms dictating past and current declines of caribou, climate change has increasing potential to exert strong direct and indirect effects now and in the future. Predicted climate effects may prevent some populations from regaining self-sustaining status, despite local conservation actions. Our review revealed several knowledge gaps, notably a lack of clarity on the spatial extent of undisturbed habitat required for caribou populations to be stable. We used outcomes from our review to demonstrate how a mechanistic understanding of population decline can inform habitat-based conservation strategies for caribou. For populations residing within highly disturbed ranges, habitat restoration is a key recommendation of current conservation strategies, yet the large spatial extent of disturbances will require prioritization of areas for restoration. Maximizing the conservation return-on-investment for caribou will require a mechanistically informed prioritization process that targets conservation actions toward the primary mechanisms underlying population decline.

KEYWORDS
boreal caribou, climate change, conservation, declining population paradigm, habitat restoration, mechanism, prioritization

INTRODUCTION

Conserving threatened and endangered species requires understanding and addressing the cause(s) of population decline. Three decades ago, Caughley (1994) described this approach as the declining population paradigm (DPP). Although conceptually straightforward, implementing the DPP can be difficult in practice and a failure to address the primary cause(s) of population decline is frequently associated with the continued imperilment of declining populations despite conservation actions (Crees et al., 2016; Thogmartin et al., 2017; Woinarski et al., 2017). Since Caughley's (1994) seminal paper, threats to biodiversity have generally increased and species are frequently impacted by multiple threats (Bonebrake et al., 2019; Tilman et al., 2017). Moreover, emerging threats and changes in the intensity of current threats can alter the relative importance of threat impacts, which can negatively affect conservation actions if only current threats are considered (Bonebrake et al., 2019; Reid et al., 2019). Within this context, we reexamine the DPP as a tool for guiding conservation actions, particularly as accelerating climate change emerges as a key threat for species already imperiled by other factors.

Caughley (1994) described the DPP as a multistep process whereby scientific investigations are conducted to determine the causes of population decline then conservation actions are developed to address these causes. In general, scientific investigations are conducted within the hypothetico-deductive method, which first entails developing hypotheses for decline based on the species' ecology and expert opinion and then testing these hypotheses experimentally. Caughley (1994) also suggested that conservation actions should be deployed in an adaptive management framework where populations are monitored posttreatment to confirm that the primary causes of decline have been identified and addressed.

The DPP was developed at a time when the specter of global climate change was only beginning to be appreciated. Consequently, Caughley (1994) suggested that causes of decline could be grouped into four categories: overkill, habitat loss/fragmentation, invasive species, and chains of extinction (e.g., the extinction of one species leads to the extinction of another). In this sense, the DPP can be thought of as retrospective and reactive because emerging threats (e.g., Reid et al., 2019) were not explicitly considered. Indeed, emerging threats are difficult to assess in the hypothetico-deductive framework inherent to the DPP because impacts from such threats may not be currently observable but instead are predicted based on data and inferences potentially collected from outside the focal system.

A further criticism of the DPP in its original derivation is its focus on "agents" of decline. Although Caughley (1994) recognized that a species may be impacted by multiple agents, there was little discussion of how agents could be linked (i.e., proximate and ultimate causes), how each agent mechanistically impacted the species, or how an agent may exert impacts through multiple mechanisms. For the purposes of this article, we define mechanism as an underlying process linking an ultimate cause (or "agent") to an observed outcome. For example, an experiment may show that habitat disturbance causes population decline but may not necessarily reveal the potential mechanisms (e.g., loss of food, invasion of novel competitors, etc.) nor their relative importance. A lack of mechanistic understanding continues to be pervasive in conservation science and likely reduces the effectiveness and cost-efficiency of conservation actions (Williams et al., 2020). In part, this deficiency may reflect the real-world difficulty in elucidating the relative importance of mechanisms when they act cumulatively or interact. Nevertheless, understanding the mechanisms of population declines and their relative importance is imperative if we are to prioritize where and when conservation actions should be deployed. Moreover, understanding mechanisms can help predict potential outcomes from emerging threats and the emergence of novel relationships (Urban et al., 2016).

Here, we revisit the DPP as a guide for developing conservation actions using the boreal ecotype of woodland caribou (hereafter, boreal caribou) as a case study. We expand upon the DPP's original derivation by focusing on mechanisms of decline, rather than agents, and explicitly consider emerging threats. Boreal caribou, which are federally listed as threatened in Canada, provide an ideal case study for a number of reasons. First, they are imperiled by multiple threats, both current and emerging (Barber et al., 2018;

Environment and Climate Change Canada, 2020; Rempel et al., 2021). Second, boreal caribou have a broad distribution and the large spatial extents of caribou ranges (i.e., areas where individual populations reside, typically >1000 km^2) present considerable conservation challenges, both logistically and financially (Johnson et al., 2019). Third, caribou ranges overlap with areas having high economic values, which has impacted the delivery of conservation actions (Fortin et al., 2020; Hebblewhite, 2017). This conflict between conservation and economics has resulted in a number of prioritization and planning efforts to optimally conserve both caribou habitat and access to natural resources (Dickie et al., 2023; Schneider et al., 2010, 2011; Vanlandeghem et al., 2021). Efforts to date, however, have rarely considered addressing the dominant mechanisms of decline in their prioritization strategies to maximize the biological benefit to caribou. By seeking to understand and consider the mechanisms underlying current and emerging threats to caribou populations, we demonstrate how habitat-based conservation strategies can be developed to optimize their cost-efficiency and effectiveness in the short and long term.

EXAMINING MECHANISMS OF CARIBOU DECLINES

Across the distribution of boreal caribou, most population declines have been attributed to unsustainable rates of predation (Environment and Climate Change Canada, 2020; Festa-Bianchet et al., 2011; McLoughlin et al., 2003). This proximate cause has been ultimately linked to landscape alteration within and adjacent to caribou range and climate change (Dawe & Boutin, 2016; Environment and Climate Change Canada, 2020; Johnson et al., 2020; Latham, Latham, McCutchen, & Boutin, 2011). The mechanisms linking increasing predation and these ultimate causes are varied, and for landscape alteration, they may depend on the type of disturbance (e.g., natural vs. human-caused; Figure 1). Moreover, landscape alteration and climate change may result in a decline in caribou populations via mechanisms other than increasing predation.

In the following sections, we examine hypothesized mechanisms explaining the decline of caribou. We specifically review the caribou literature, with an emphasis on studies of boreal caribou, to assess the relative support and potential importance of each putative mechanism. To do so, we evaluated whether demographic effects (e.g., lowered survival or recruitment) have been reported for a given mechanism and whether such effects have been explicitly linked to population growth rates (λ) of caribou. This approach necessarily differs from the classical definition of the DPP, where experimental studies would be conducted for each mechanism. Conducting such study is logistically and economically difficult because of the large spatiotemporal scales required to effectively assess caribou demographic impacts;

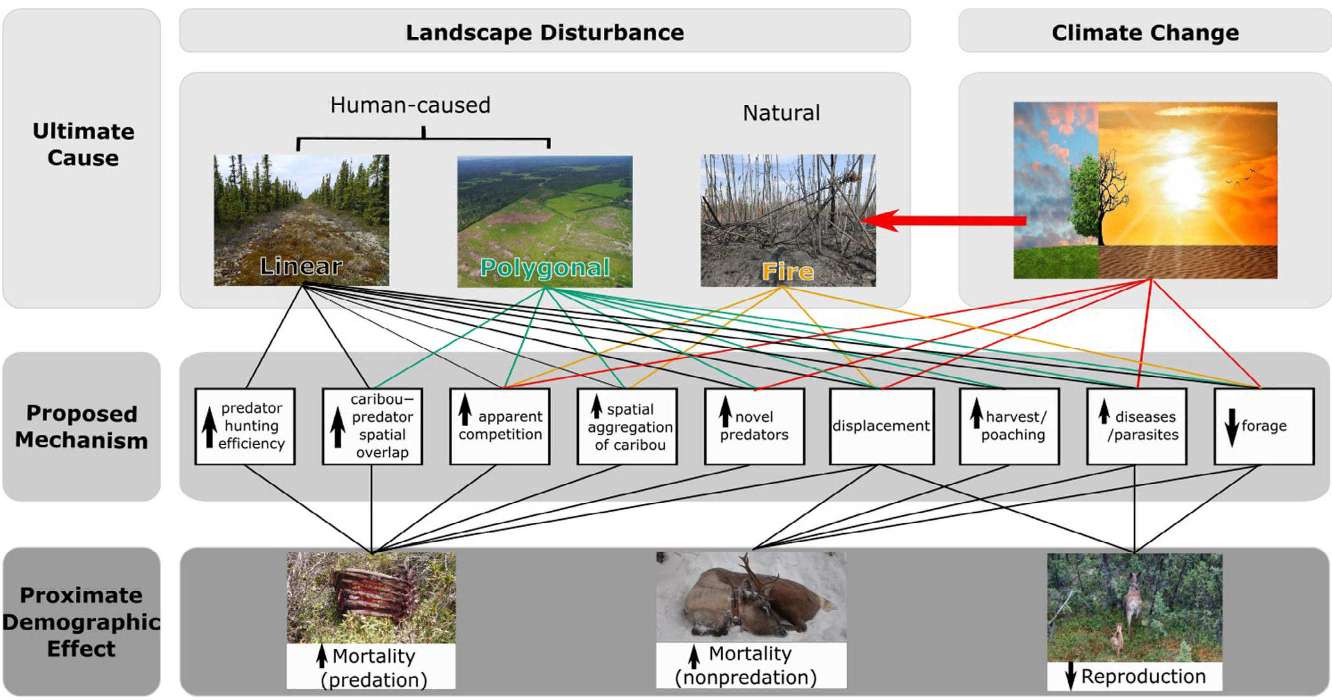

FIGURE 1 Proposed mechanisms linking landscape disturbance and/or climate change to the demography of boreal caribou.

consequently, these studies are rare (e.g., see McNay et al., 2022; Serrouya et al., 2019). Nevertheless, our approach identifies key knowledge gaps where experimental studies may be needed to discern a mechanism's relative importance and to inform the current and future efficacy of conservation strategies.

MECHANISMS ASSOCIATED WITH LANDSCAPE DISTURBANCE

Boreal caribou occur within the boreal forests of Canada, an area frequented by natural (Zhang & Chen, 2007) and human-caused disturbances (Hebblewhite, 2017). Within this distribution, boreal caribou generally prefer older forests and low-productivity peatlands, a spatial strategy that reduces predation risk by separating caribou from other ungulates (e.g., moose [*Alces alces*] and deer [*Odocoileus* spp.]) and their generalist predators (e.g., wolves [*Canis lupus*]; Courbin et al., 2013; James et al., 2004; Rettie & Messier, 2000). Multiple analyses have demonstrated a negative correlation between caribou λ and the extent of disturbances within their range (Environment and Climate Change Canada, 2020; Johnson et al., 2020; Serrouya et al., 2021; Sorensen et al., 2008). This relationship underpins the definition of critical habitat in Canada's recovery strategy for boreal caribou, the protection of which requires limiting the disturbance footprint (human-caused disturbances buffered by 500 m and forest fires ≤40 years old) within caribou range to <35%, a target equating to a 60% probability that a population will be self-sustaining (Environment Canada, 2008; Environment and Climate Change Canada, 2020; Johnson et al., 2020). Different types of disturbance, however, may demographically impact caribou through different mechanisms (Figure 1). Discerning the relative influence of different disturbance types and mechanisms is often difficult because most caribou ranges are affected by multiple disturbance types. Although the cumulative effects of multiple disturbances and types are complex and may be additive, interactive, or nonlinear, we consider natural and human-caused disturbances separately and further subdivide human-caused disturbances by shape (polygonal or linear). This reductionist approach is necessary for not only tractability of explanation but also ascribing mechanistic outcomes to disturbance types.

Human-caused disturbances

Human-caused disturbances can be classified as polygonal or linear. Polygonal disturbances (PDs) include agricultural clearings, cutblocks, and well pads. Linear disturbances (LDs) include roads, pipelines, and seismic lines (narrow lines created for hydrocarbon exploration). Although we consider the two types separately, PDs are often created alongside LDs (e.g., logging roads and cutblocks) and likely impact caribou concurrently, though LDs may exist across large areas without any nearby PDs.

Mechanisms of polygonal disturbances

Negative correlations between caribou demography and PDs have long been recognized (e.g., Bergerud, 1974), and numerous studies support this relationship (e.g., Courtois et al., 2007; Seip, 1992; Serrouya et al., 2021; Vors et al., 2007). We considered eight mechanisms that could plausibly link PDs with caribou population declines: apparent competition, the expansion of novel predators, increased caribou–predator spatial overlap, spatial clumping of caribou, displacement, increased harvest and poaching, increased transmission of diseases and parasites, and decreased food availability (Figure 1). Among these mechanisms, apparent competition has the most empirical support (Table 1). Only two mechanisms—apparent competition and the expansion of novel predators—have been empirically linked to population declines of caribou. Four mechanisms—spatial clumping of caribou, displacement, increased transmission of disease and parasites, and decreased food availability—have theoretical support but have not been evaluated empirically.

Apparent competition is considered a primary mechanism for the decline of caribou populations (Environment and Climate Change Canada, 2020; Festa-Bianchet et al., 2011; Hebblewhite, 2017) and PDs are likely an ultimate driver of this process (Seip, 1992). Apparent competition is a multitrophic mechanism whereby PDs increase forage for moose and deer, resulting in positive numeric responses in these ungulates and their generalist predators, the latter of which opportunistically predate caribou at unsustainable rates (Holt, 1977; Seip, 1992). Individually, each prediction of apparent competition has substantial support (e.g., PDs increase densities of moose and deer: Côté et al., 2004; Fisher et al., 2020; Potvin et al., 2005; Rempel et al., 1997; Serrouya et al., 2021; increased ungulate densities increase predator densities: Fuller, 1989; Fuller et al., 2003; Messier, 1994; Schwartz & Franzmann, 1991; increased predator densities correlate with caribou population decline: Bergerud, 1988; Serrouya et al., 2021). Recent studies have also evaluated these predictions concurrently and all showed negative demographic impacts to caribou (e.g., decreased juvenile recruitment, Frenette et al., 2020; decreased caribou λ, Fryxell et al., 2020; Serrouya et al., 2021).

TABLE 1 Mechanisms associated with polygonal and linear disturbances, evidence for their proposed demographic effects on boreal woodland caribou, and a ranking of their relative importance.

Mechanism by disturbance type	Observed demographic effects	Quantified link to $\lambda < 1.0$		Relative importance
		Empirical	Simulated	
Polygonal				
Apparent competition	Yes[1–3]	Yes[1–3]	Yes[4,5]	High
Expansion of novel predators	Yes[2]	Yes[2]	...	High
Increased caribou–predator spatial overlap	Yes[6]	...	...	High
Increased harvest and poaching	Yes[7,8]	...	...	Low
Spatial clumping of caribou	No	...	...	Low
Displacement	No	...	...	Low
Increased disease and parasites	No	...	...	Low
Decreased food availability	No	...	...	Low
Linear				
Increased caribou–predator spatial overlap	Yes[9–11]	...	Yes[12]	High
Increased predator hunting efficiency	Equivocal[13–15]	...	Yes[12,16,17]	High
Expansion of novel predators	Yes[18–20]	...	...	High
Apparent competition	No	...	...	Low
Spatial clumping of caribou	No	...	...	Low
Displacement	No	...	...	Low
Increased harvest and poaching	No	...	...	Low
Increased disease and parasites	No	...	...	Low
Decreased food availability	No	...	...	Low

Note: References (numbers in superscript) are: 1, Serrouya et al. (2021); 2, Frenette et al. (2020); 3, Fryxell et al. (2020); 4, Vanlandeghem et al. (2021); 5, Rempel et al. (2021); 6, Peters et al. (2013); 7, Rudolph et al. (2017); 8, Schmelzer et al. (2020); 9, DeMars and Boutin (2018); 10, James and Stuart-Smith (2000); 11, Mumma et al. (2018); 12, Serrouya et al. (2020); 13, DeCesare et al. (2012); 14, McPhee et al. (2012); 15, Dickie et al. (2020); 16, McCutchen (2007); 17, Spangenberg et al. (2019); 18, Latham et al. (2013); 19, Pattison et al. (2020); 20, Fisher and Burton (2018).

The northward expansion of novel predators (e.g., coyotes [*Canis latrans*] and cougars [*Puma concolor*]) also has empirical support as a driver of population declines in caribou. Within the boreal forest, coyotes have shown selection for PDs (cutblocks: Boisjoly et al., 2010; well sites: Toews et al., 2018), potentially contributing to coyote distribution expanding into caribou range (Frenette et al., 2020; Latham et al., 2013). In eastern Canada, coyote predation has had a large negative effect on calf survival of caribou (e.g., ~64% of known mortalities) and is thought to be additive to bear predation (Frenette et al., 2020). Cougars are also expanding northward (Knopff et al., 2014) and cougar predation of mountain caribou is now occurring in areas where it has not been previously reported (White et al., 2020). PDs are likely facilitating cougar expansion by increasing the extent of edge habitats, which cougars select (Knopff et al., 2014), and by increasing deer abundance (Pierce et al., 2012). Although cougar predation of boreal caribou has yet to be documented, cougar predation has been implicated in population declines of southern mountain caribou (Kinley & Apps, 2001; Serrouya et al., 2015).

Two other PD mechanisms—increased caribou–predator spatial overlap and increased harvest by humans—have evidence of negative demographic effects, but have not been directly related to caribou λ. For the spatial overlap mechanism, PDs create early seral conditions that may draw other ungulates and their generalist predators into caribou range (Courbin et al., 2013; Peters et al., 2013). PDs may also increase spatial overlap between caribou and bears independent of changes in the populations of other ungulates. As omnivores, bear populations may increase in response to the forage provided by PDs (Brodeur et al., 2008; Schwartz & Franzmann, 1991) and increasing bear numbers may result in a greater proportion of bears "spilling over" into caribou habitat (Jeffries & Lawton, 1984). Bears may also opportunistically encounter caribou while moving between patches of early seral vegetation (Bastille-Rousseau et al., 2011).

PDs and their associated road networks may also facilitate increased harvest and poaching of caribou (Courtois & Beaumont, 1999; Rempel et al., 1997). In most ranges of boreal caribou, sport hunting has been banned for at least two decades, although indigenous harvest still occurs and is protected by treaty and inherent rights (Rudolph et al., 2017). Nonindigenous incidental harvest also occurs, particularly where winter ranges overlap between boreal caribou and other caribou ecotypes that may be legally hunted (Schmelzer et al., 2020). For most populations of boreal caribou, the demographic impacts of harvest remain largely unknown (Environment and Climate Change Canada, 2020; but see Schmelzer et al., 2020, for an example).

The remaining mechanisms associated with PDs have theoretical support but lack empirical evidence of demographic effects. The spatial clumping mechanism refers to how PDs may affect caribou distribution, potentially making them more predictable to predators. To reduce predator encounters, boreal caribou form small groups for most of the year and roam over large ranges, making them unpredictable in time and space. PDs may impact this strategy because caribou generally avoid PDs (Courtois et al., 2007; DeCesare et al., 2012; Faille et al., 2010; Smith et al., 2000), resulting in a more clumped and predictable distribution of caribou and potentially increasing predation risk (DeMars et al., 2016; Fortin et al., 2013). PDs also may change caribou distribution at a larger scale by causing shifts in seasonal or annual home ranges (the displacement mechanism; Faille et al., 2010; MacNearney et al., 2016). Such shifts could displace caribou into suboptimal habitat, potentially affecting forage availability or increasing predation risk by forcing individuals into novel environments.

PDs may contribute to increased transmission of diseases and parasites to caribou by facilitating increased spatial overlap with other ungulates (Fisher et al., 2020; Peters et al., 2013). For example, increasing occurrences of moose in caribou range have been implicated in high rates of winter tick loads within populations of boreal caribou (Bondo et al., 2019). White-tailed deer (*Odocoileus virginianus*) expansion, which can negatively impact caribou by multiple mechanisms, may increase the prevalence of meningeal worm (Anderson, 1972) and chronic wasting disease (Mysterud et al., 2019), both of which are highly pathogenic to caribou. Although the threat to caribou from diseases and parasites is likely increasing, their current demographic effects are not well understood.

The final mechanism, decreased food availability, is perhaps the most equivocal. By decreasing the extent of mature forests, PDs could decrease lichen availability, which is a primary food source for caribou during winter (Thompson et al., 2015). Bergerud (2007) has disputed lichen limitation as a mechanism of population decline, pointing out that caribou can survive in environments where lichens are absent and that their lichen-dominated diet is a consequence of their strategy of spatial separation from predators. Nevertheless, if caribou avoid PDs and their adjacent edge habitats (Courtois et al., 2007; Dyer et al., 2001; Fortin et al., 2013), then risk-sensitive foraging could reduce the area used by caribou and limit food availability, potentially leading to negative demographic outcomes. Risk-sensitive foraging has been postulated for lowered nutritional condition in one population of mountain caribou, which demonstrated an increased λ with supplemental feeding (Heard & Zimmerman, 2021). Another study, however, reported that nutritional stress was not a cause of decline in several populations of mountain caribou (McLellan et al., 2012). To date, this mechanism has not been evaluated in boreal caribou.

Polygonal disturbances: Management implications

Reducing PDs within caribou range is a primary recommendation for recovering caribou populations (Environment and Climate Change Canada, 2020; Johnson et al., 2020). For highly disturbed ranges with declining caribou populations, understanding the above mechanisms can help prioritize where PDs should be restored or avoided, potentially increasing the effectiveness of conservation strategies. Because most mechanisms have a strong spatial component (e.g., increased caribou–predator spatial overlap; increased disease transmission), priority should be given to reducing PDs within and immediately adjacent to caribou habitat and to maintaining large, contiguous tracts of caribou habitat that are located far from PDs (Courbin et al., 2009). Additionally, forest management could play a role in the relative value of postharvest conditions for deer and moose. For example, silviculture systems could focus reforestation within caribou ranges on less palatable species (i.e., spruce trees [*Picea* spp.]) and regenerating deciduous forest far from areas of high caribou use. The focus on PDs within caribou range, however, may have reduced effectiveness against apparent competition because the scale at which altered predator–prey dynamics affect caribou demography may exceed range boundaries. Indeed, the size of caribou ranges can vary by an order of magnitude, which highlights how a conservation strategy that focuses only within range may not align with the scale at which a mechanism operates. Understanding the relevant spatial scale(s) of apparent competition is a key knowledge gap in caribou conservation, particularly given its relatively strong support as a primary driver of caribou population declines. Despite this uncertainty, it is highly probable that for small, isolated caribou ranges, the scale of conservation strategies will need to exceed current range boundaries to effectively reduce apparent competition and achieve self-sustaining status for caribou.

Mechanisms of linear disturbances

LDs are a common type of disturbance within Canadian boreal forests (Dabros et al., 2018; Poley et al., 2022). The spatial extent and density of each LD type vary depending on a region's dominant form of resource extraction. In western Canada, seismic lines are the most widespread type (DeMars & Boutin, 2018; Dickie et al., 2017), whereas secondary roads related to forestry are most prevalent in eastern ranges (Dussault et al., 2012; Kittle et al., 2017; Vors et al., 2007). Within most ranges, the actual physical footprint of LDs is relatively small (e.g., <5% of total area; Latham, Latham, Boyce, & Boutin, 2011; Pattison et al., 2016), yet their proposed zones of influence on caribou behavior can extend ≥400 m beyond the disturbed area (Dyer et al., 2001; Nagy, 2011). As such, demographic models assessing disturbance effects have included the spatial adjacency of habitats, also known as buffers, around human-caused disturbances, including LDs (Environment and Climate Change Canada, 2020; Johnson et al., 2020). Few studies have documented or assessed the mechanisms that explain the potential negative demographic outcomes for caribou that use habitats adjacent to LDs (e.g., Apps et al., 2013; James & Stuart-Smith, 2000). Even without buffers, analyses indicate that LD density within caribou range is negatively correlated with caribou λ (Boutin & Arienti, 2008).

LDs may impact caribou demography through mechanisms similar to those associated with PDs (Table 1). To date, no LD mechanism has empirical evidence directly linking it to caribou population declines, although simulation studies suggest declines could result from LD-mediated effects on predator hunting efficiency and spatial overlap with caribou (Serrouya et al., 2020). Two mechanisms—increased caribou–predator spatial overlap and the expansion of novel predators—have demonstrated demographic effects on caribou, whereas the rest have only theoretical support.

Much of the current literature on LD effects has focused on how these features may alter predator hunting behavior. Several studies have shown that predators, particularly canids, select LDs in forested systems (DeMars & Boutin, 2018; Dickie et al., 2017, 2020; Kittle et al., 2017; Latham, Latham, Boyce, & Boutin, 2011), likely because LDs enhance movement efficiency. This behavior may impact caribou populations via two mechanisms. First, predators may follow LDs into caribou habitat increasing their probability of encounter with caribou (DeMars & Boutin, 2018; Dickie et al., 2020; James & Stuart-Smith, 2000; Mumma et al., 2018), potentially leading to negative demographic effects (e.g., lowered survival of neonate calves, DeMars & Boutin, 2018; lowered adult survival, Apps et al., 2013; McKay et al., 2021). Such effects may be exacerbated if caribou use LDs as movement corridors, as some studies have shown (Dickie et al., 2020; Serrouya, Kellner, et al., 2017). Second, by moving faster on LDs, predators may increase their hunting efficiency by encountering and killing prey more often (Dickie et al., 2017; McKenzie et al., 2012; Vander Vennen et al., 2016). Several simulation studies support this prediction (McCutchen, 2007; Serrouya et al., 2020; Spangenberg et al., 2019), but empirical evidence of an increased kill rate is lacking (e.g., see DeCesare, 2012; McPhee et al., 2012). Serrouya et al. (2020) evaluated the relative importance of these two mechanisms by modeling wolf–prey dynamics in a simulated landscape. Model outputs suggested that LDs had a higher negative impact on caribou demography by increasing caribou–wolf spatial overlap than that by increasing wolf movement efficiency (53% decline in the equilibrium density of caribou due to spatial overlap vs. 41% decline from increased movement rate).

A second, linked prediction of increased hunting efficiency is that the increase in kill rates afforded by LDs will increase predator abundance. This relationship is likely dependent on prey densities and density-dependent mortality of predators (Serrouya et al., 2020). For the former, when prey densities are high, time budgets of predators are dominated by prey handling, and thus moving faster to the next prey has minimal influence on the kill rate. Conversely, at low prey densities, prey searching dominates predator time budgets and LDs can have higher influence on kill rates by increasing the search rate. Increasing kill rates, in turn, can increase predator populations. Empirical studies assessing these relationships have used territory size as a surrogate for predator abundance. In general, these studies have shown a negative correlation between territory sizes of wolves and LD density (Dickie et al., 2022; Kittle et al., 2015; Sells et al., 2021), suggesting that increasing LD density may facilitate higher predator abundances because more territories can be "packed in" at a landscape scale. Moreover, this effect is more pronounced at low prey densities.

Beyond potential changes in predator behavior, LDs may impact caribou through other mechanisms, including those that are movement-based (e.g., the expansion of novel predators, increased harvest/poaching, and increased diseases/parasites) and forage-based (e.g., apparent competition, decreased caribou food). For the most part, these mechanisms have received less attention and their demographic effects have not been quantified. Some mechanisms are similar to those described for PDs. For example, caribou avoidance of anthropogenic features, which includes LDs (DeMars & Boutin, 2018; Dyer et al., 2001; Mumma et al., 2018), may make them more spatially aggregated and predictable to predators (DeMars et al., 2016; Fortin et al., 2013). Some LDs (e.g., roads and aboveground pipelines) may further exacerbate the spatial clumping mechanism by functioning as semipermeable barriers to caribou movement (Leblond et al., 2013; Muhly et al., 2015).

The role of LDs in movement-based mechanisms relates to how LDs facilitate and direct animal and human movement (DeMars & Boutin, 2018; Dickie et al., 2017). Novel predators such as coyotes and cougars have shown selection for LDs (Fisher & Burton, 2018; Latham et al., 2013; Pattison et al., 2020), a response that likely facilitates their movements northward into caribou range. Other ungulates may also follow LDs into caribou habitat, potentially increasing parasite and disease transmission to caribou (Bondo et al., 2019; Mumma et al., 2018). For humans, LDs allow travel into previously inaccessible areas, which increases harvest pressure on ungulates including caribou (Environment and Climate Change Canada, 2020; Pigeon et al., 2016; Plante et al., 2017).

The role of LDs in forage-based mechanisms is equivocal. For apparent competition, LDs are likely less influential than PDs as the amount of early seral forage created by LDs is modest owing to their relatively small footprint (e.g., <5% of total area; Latham, Latham, Boyce, & Boutin, 2011; Pattison et al., 2016). This reasoning may explain why moose densities did not correlate with LD densities in northeastern British Columbia (Mumma et al., 2018). For white-tailed deer, there is evidence to suggest that LD forage subsidies may enhance their reproduction (Fisher & Burton, 2021), yet in the same study area, deer distribution was influenced by PDs more than LDs (Darlington et al., 2022; Fisher et al., 2020). The small footprint of LDs may also result in only modest losses in caribou forage, although boreal caribou have been reported to avoid LDs by 250–400 m (Dyer et al., 2001; Nagy, 2011) and such risk-sensitive behavior may further reduce forage availability, particularly in ranges with high LD density. As discussed under PD mechanisms, the potential demographic effects of risk-sensitive foraging are unknown for boreal caribou (but see Heard & Zimmerman, 2021).

Linear disturbances: Management implications

Restoring LDs has become a management priority because of their negative correlation with caribou demography (Boutin & Arienti, 2008; DeMars & Boutin, 2018; Mumma et al., 2018). However, LDs have a vast spatial extent, particularly in western Canada, which presents a significant challenge when trying to restore areas that are large enough in size to meaningfully impact caribou demography (Johnson et al., 2019; Nagy-Reis et al., 2021; Serrouya et al., 2020). Additional challenges include continued public use of LDs that undermines vegetation regrowth (Pigeon et al., 2016), high economic costs (e.g., >$12,500/km; Filicetti et al., 2019), and the significant logistical difficulties with restoring LDs in remote areas that are accessible only during winter. For the latter two points, it should be noted that LD restoration is a relatively new activity and technical innovation is ongoing, which could lead to significant increases in efficiency. Nonetheless, in highly disturbed ranges, current economic and logistical challenges require that LDs be prioritized for restoration, and understanding the relative importance of each mechanism can inform this process. Although quantitative assessments and comparisons of demographic impacts are lacking for most LD mechanisms, our review suggests that LDs in peatlands and old-growth forests should receive a high priority to reduce caribou–predator spatial overlap and restore spatial refugia for caribou. Even with this strategy, challenges remain as LDs in these areas are the slowest to regenerate (van Rensen et al., 2015) and difficult to restore (Filicetti et al., 2019; St-Pierre et al., 2021), and a high proportion of LDs will likely need to be restored to have positive demographic effects (McCutchen, 2007; Serrouya et al., 2020; Spangenberg et al., 2019).

In the context of the DPP, LD restoration will be ineffective for stabilizing caribou populations in the short term (e.g., within 10–15 years; Johnson et al., 2019) because of the large spatial scales necessary to achieve appreciable demographic effects. Recently, LDs have been the focus of "functional restoration" techniques, such as felling trees across LDs to reduce predator use or movement speed (Keim et al., 2021). These techniques aim to rapidly restore pre-disturbance predator–prey dynamics without necessarily returning the area to a pre-disturbed state (i.e., older forest). Although such techniques have shown promise in reducing caribou–predator encounter rates in the short term (e.g., ≤2 years after treatment deployment; Keim et al., 2021), the long-term efficacy of this approach is unknown and treatments will still need to be deployed over large spatial scales, which may take considerable time and resources. Consequently, it is unlikely that LD restoration by itself will prevent the extirpation of small, rapidly declining populations. Nevertheless, if the long-term management objective is to achieve self-sustaining caribou populations, then limiting LD creation and actively restoring existing LDs will be necessary components of a comprehensive management strategy. Despite the negative demographic effects associated with LDs, a decelerating rate of LD density—or even a net-zero rate of LD creation versus restoration—has been achieved in few caribou ranges to date (e.g., one of nine ranges in Alberta, Nagy-Reis et al., 2021; Rudolph et al., 2017).

MECHANISMS ASSOCIATED WITH NATURAL DISTURBANCE

By increasing the extent of early seral conditions, natural disturbances can impact caribou through mechanisms similar to those associated with anthropogenic disturbances. In boreal forests, the dominant form of natural disturbance is fire. Return intervals for fire vary depending on the region but are generally shorter in the west (e.g., <100 years in Alberta, Larsen, 1997; >250 years in Quebec, Bouchard et al., 2008). Within Canada's federal recovery strategy for boreal caribou, demographic impacts from fires ≤40 years old are considered additive to anthropogenic disturbances (Environment Canada, 2008; Johnson et al., 2020). Management options for caribou must therefore consider the region's natural disturbance regime (e.g., fire return interval) and the extent of regenerating burns (Johnson et al., 2020; see *Natural disturbances: Management implications* for further discussion). Although teasing apart the relative influences of natural versus anthropogenic disturbances can be difficult, particularly in highly disturbed landscapes, demographic effects of fires appear to be weaker (Environment Canada, 2008; Johnson et al., 2020; Superbie et al., 2022), which likely reflects underlying differences in the causal mechanisms.

Boreal caribou have evolved with fire, and over the long term, fire is an important process within caribou range because of its role in regenerating lichens (Dunford et al., 2006; Silva et al., 2019). However, in the shorter term (e.g., <40- to 50-year postfire), fires have negative impacts on caribou primarily through forage-based mechanisms that influence both caribou and their apparent competitors (Figure 1). Early literature on caribou–fire dynamics suggested that fires decreased lichen abundance, at least in the first 40-year postfire (Edwards, 1954; Schaefer & Pruitt, 1991). Bergerud (1974) disputed this mechanism as a cause of population decline, arguing that there was little evidence to indicate a lowered nutritional condition in caribou. Behavioral responses of caribou also do not support forage loss as a cause of decline as individuals often do not shift their home ranges postfire (Dalerum et al., 2007; Faille et al., 2010), and they have been shown to use young burns (e.g., <5 years old; Lafontaine et al., 2019; Silva et al., 2020; Superbie et al., 2022). Instead of forage loss, Bergerud (1974) suggested population declines were due to increased natural predation resulting from increasing moose and deer populations. Over the last three decades, apparent competition has been increasingly accepted as the primary mechanism for explaining negative impacts of fire on caribou demography (Bergerud, 1996; Festa-Bianchet et al., 2011; Johnson et al., 2020; Seip, 1992). Recent studies, however, have suggested that the relative strength of fire-mediated apparent competition may vary regionally and may be weak in low-productivity systems (e.g., peatlands, DeMars et al., 2019; Johnson et al., 2020; Neufeld et al., 2021; Superbie et al., 2022). These weak effects are unsurprising as caribou have existed within boreal forests for millennia under historical fire regimes. Climate change may challenge this evolved relationship if the frequency and spatial extent of fire increases and/or a drying climate changes the trajectory of postfire succession (Baltzer et al., 2021).

Early seral vegetation that follows fire may impact caribou through other mechanisms. Moose, deer, and their generalist predators may be drawn into burns within caribou range, increasing caribou–predator spatial overlap (Bergerud, 1996; Seip, 1992). This mechanism is particularly relevant for bears, which may opportunistically prey on caribou calves while moving among early seral patches containing suitable forage (e.g., berries and forbs; Bastille-Rousseau et al., 2011; Schwartz & Franzmann, 1991). Increasing predation from bears could explain why fires appear to have a greater negative effect on caribou via reduced juvenile recruitment rather than lowered survival of adult females (Johnson et al., 2020). As with apparent competition, the relative strength of caribou–predator spatial overlap likely depends on site-specific primary productivity, which dictates the type and amount of forage generated postfire (DeMars et al., 2019; Superbie et al., 2022). If burned areas are highly used by other ungulates, fires may further increase predation risk to caribou if they avoid these areas and become more spatially aggregated (Courtois et al., 2007; Dalerum et al., 2007; DeMars et al., 2016; Fortin et al., 2013; Konkolics et al., 2021). As discussed previously, the strength of this mechanism is unknown but likely depends on the spatial extent of burns and other (anthropogenic) disturbances.

Natural disturbances: Management implications

Habitat-based management strategies for boreal caribou are currently focused on minimizing disturbances within caribou range (Environment and Climate Change Canada, 2020). The extent of disturbance is calculated as the cumulative area of fires ≤40 years old and the buffered (500 m) anthropogenic footprint. Recent studies, however, suggest that caribou can coexist with fire to a much greater degree than anthropogenic disturbances (Neufeld et al., 2021; Stewart et al., 2020; Superbie et al., 2022). It is currently unclear as to what drives the differences in effect magnitudes, but it may be due to the additional impacts of LDs associated with the anthropogenic footprint (Festa-Bianchet et al., 2011) or contrasting successional trajectories (Nguyen-Xuan et al., 2000).

Under the DPP, conservation strategies should prioritize the management of anthropogenic disturbances over fires because of the latter's weaker effects on caribou demography (Johnson et al., 2020; Stewart et al., 2020). Nevertheless, because demographic outcomes from fire are generally negative for caribou, these effects need to be considered when managing disturbances within caribou range. For ranges highly altered by anthropogenic disturbance, fires may accelerate population declines. Similarly, for ranges with extensive burns ≤40 years old, small increases in the extent of anthropogenic disturbances could trigger declines in previously stable populations. Thus, disturbance management requires a flexible approach where targets for allowable human-caused disturbances (e.g., forest harvest) may need to be reduced to compensate for increased natural disturbances if they occur. Despite these cautions, fires can provide some benefits as they are agents of restoration in removing anthropogenic disturbances from the landscape, particularly seismic lines (Filicetti & Nielsen, 2018, 2022). Ultimately, effective range management will require a better understanding of how fires interact with anthropogenic disturbances to impact caribou demography. Such understanding is particularly important given that climate change is predicted to increase the extent, frequency, and intensity of fires in the boreal forest (Baltzer et al., 2021; Bowman et al., 2020).

MECHANISMS ASSOCIATED WITH CLIMATE CHANGE

Climate strongly influences the distribution of most species, including caribou. At the last glacial maximum, the southern limit of caribou distribution in North America extended as far south as modern-day Alabama (Churcher et al., 1989) but has since shifted northward as the climate warmed (Flagstad & Røed, 2003). Bergerud (2007) has suggested that the southern limit of caribou distribution is determined by the distribution and abundance of apparent competitors (e.g., moose and deer), which are both dictated by climatic effects on winter severity and primary productivity. If we accept that this mechanism is universal and persistent, caribou distribution is likely to further contract northward as Canada's boreal forest potentially becomes "greener" (Dearborn & Baltzer, 2021) with shorter, warmer winters (Dawe et al., 2014).

Rapid climate change is an emerging and long-term threat to caribou, but the relative magnitude and timing of its impacts on caribou population dynamics are still uncertain. Evaluating climate change effects on observed declines of caribou over the last 50–70 years is not generally possible because, in many ranges, the onset of human-caused climate change coincides with the onset of human-caused landscape disturbance and subsequent increase in hunting mortalities (Bergerud, 1974; IPCC, 2014; Schaefer, 2003; Vors et al., 2007). One recent retrospective analysis suggested that anthropogenic disturbance had a stronger effect than climate change (Neilson et al., 2022). However, impacts from climate change are likely to strengthen in the future (e.g., Barber et al., 2018; Deb et al., 2020; Rempel et al., 2021). Some impacts are already evident. For example, in western Canada, less severe winters interacting with landscape disturbance have facilitated the expansion of white-tailed deer into the boreal forest (Dawe & Boutin, 2016; Fisher et al., 2020; Laurent et al., 2021). This expansion has contributed to increased wolf densities and subsequent increased predation of caribou (Latham, Latham, McCutchen, & Boutin, 2011). In eastern Canada, where white-tailed deer have historically occurred at low densities within caribou range (Kennedy-Slaney et al., 2018), this effect has been less severe, possibly because eastern ranges have less extensive and intensive anthropogenic disturbance (Environment and Climate Change Canada, 2020) as well as regional differences in rates of climate change (IPCC, 2014). Nevertheless, deer densities are expected to increase within eastern ranges of caribou as winters become less severe (Kennedy-Slaney et al., 2018). Climate change may further contribute to population increases of moose and deer by increasing primary productivity within the boreal forest (Serrouya et al., 2021). This climate effect requires further investigation as debate persists as to whether a warming climate will lead to "greening" or "browning" (i.e., drying and early plant senescence) of the boreal forest (Dearborn & Baltzer, 2021; Sulla-Menashe et al., 2018).

The climate-influenced expansion of apparent competitors brings additional threats to boreal caribou. These include the expansion of novel predators (i.e., cougars and coyotes), which may track the northward expansion of deer (Mallory et al., 2013; Pierce et al., 2012). Expanding populations of apparent competitors also increase the risk of disease and parasite transmission to caribou (Kutz, 2004; Morales-Castilla et al., 2021). The risk of chronic wasting disease is particularly acute as this disease can have a relatively high prevalence in white-tailed deer populations (Smolko et al., 2021), and boreal caribou may be susceptible to this fatal disease where they overlap with deer (Arifin et al., 2020).

Climate change may also impact caribou demographics through more direct mechanisms (i.e., not mediated by community interactions). A warming climate will likely cause spatiotemporal changes in resource availability and quality, potentially impacting survival and reproduction (Post & Forchhammer, 2008; Sæther, 1997). For example, survival of adult female caribou has been negatively correlated with weather events associated with icing (freezing rain in autumn, Schmelzer et al., 2020; increased variability of winter temperatures, DeMars et al., 2021), and such events are predicted to increase in frequency with climate change (Newton et al., 2021). Potential impacts are not restricted to winter. Juvenile recruitment has been negatively correlated to warmer growing seasons that lead to early plant senescence in autumn (DeMars et al., 2021), an important period of resource acquisition for capital breeders such as caribou. Although current impacts from these direct mechanisms are likely secondary to the other more indirect mechanisms previously discussed (e.g., apparent competition), there is considerable uncertainty as to how the magnitude of these direct impacts may change as climate change progresses (DeMars et al., 2021).

Climate change: Management implications

Climate change presents significant challenges when using the DPP to guide conservation actions. Unlike human-caused disturbances, which ostensibly can be restored, human-caused climate change cannot be fully addressed through regional conservation or management strategies. Moreover, climate change may reduce the efficacy of conservation actions targeted toward human-caused disturbances. For example, if climate change slows or halts natural regeneration or changes the successional trajectory of disturbances, then active restoration may become necessary for an increasing proportion of disturbance features (Taylor et al., 2020). A further concern is that conservation actions deployed now may be undermined by climate change in the future (Gilbert et al., 2020). Some impacts, such as the expansion of apparent competitors, may be amenable to management actions (e.g., Serrouya, McLellan, et al., 2017), but such actions may need to be continued in perpetuity over large spatial scales if maintaining the current distribution of caribou is a priority. Other impacts may be more logistically difficult and/or expensive to mitigate, such as widespread habitat change due to drying and/or an increased frequency of fire (Baltzer et al., 2021; Barber et al., 2018; Palm et al., 2022). As an emerging threat, climate change may further confound conservation strategies because of uncertainty in the evolving magnitude of impacts. Recent simulation studies have attempted to predict future impacts of climate change on caribou (Barber et al., 2018; Bauduin et al., 2018; Rempel et al., 2021), but such forecasts still contain a high degree of uncertainty and conservation strategies are rarely proactive, particularly with respect to "what if" scenarios (Fuller et al., 2020). Nevertheless, given the strong influence that climate has on caribou distribution, it is becoming increasingly probable that populations at the southern limit of current caribou distribution will not be self-sustaining as climate change progresses.

INCORPORATING MECHANISM INTO CONSERVATION STRATEGIES

The primary objective of Canada's federal recovery strategy for boreal caribou is to achieve or maintain self-sustaining status for all extant populations (Environment and Climate Change Canada, 2020). Because population declines are primarily attributed to landscape disturbance, key management recommendations are focused on habitat protection and restoration. These recommendations, however, are not trivial to enact because of the high number of declining populations, the spatial extents of caribou ranges, and the extensive area of disturbances within many ranges. For populations to have a reasonable probability (60% chance) of being self-sustaining, the recovery strategy stipulates that landscape disturbances (human-caused and natural) should comprise <35% of caribou range. For highly disturbed ranges, achieving this threshold will take decades—even with intensive restoration efforts—and incur substantial costs (e.g., >$100 million per range, Johnson et al., 2019).

Given the challenges of restoring habitat over a large spatial extent, a prioritization strategy will be necessary to maximize conservation outcomes (Bottrill et al., 2009). We suggest that such strategies will be more effective for caribou if they are informed by an understanding of the mechanisms potentially driving population declines now and in the future. Maximizing conservation outcomes should always be a central driver in any prioritization process and, as such, requires clearly defined rules and objectives to prevent a progressive decline in responsibility to undertake conservation actions (Johnson et al., 2022; Wilson & Law, 2016). Our purpose here is not to define such goals and objectives but to highlight how a mechanistic understanding should inform conservation actions, including habitat restoration.

To illustrate a potential prioritization framework, we use caribou ranges in Alberta. Many ranges in this region are extensively disturbed by natural resource development, which has contributed to most caribou populations being classified as not self-sustaining (Environment and Climate Change Canada, 2020). In a few ranges, efforts to restore habitat have already been initiated (Dickie et al., 2021; RICC, 2020; Tattersall et al., 2020), though restoration rates are still generally below rates of habitat loss (Nagy-Reis et al., 2021).

We begin by prioritizing areas within caribou range. We use the Cold Lake range as an example and focus on seismic lines as these are the most pervasive form of disturbance (Dickie et al., 2017). We further focus on prioritizing restoration to address the mechanism of increased caribou–predator spatial overlap facilitated by LDs. We compare two prioritization approaches: one termed "gain-in-undisturbed" (GIU) approach, which focuses on restoring seismic lines to meet the federal recovery strategy's 35% disturbance threshold as quickly as possible with no consideration of the spatial overlap mechanism; and the other termed "gain-in-refugia" (GIR) approach, which prioritizes the restoration of seismic lines within peatlands to reduce predator movement into and within this habitat type, which when intact provides refugia for caribou (James et al., 2004; Rettie & Messier, 2000). For both approaches, we keep the prioritization process relatively simple because our objective is not to provide a prioritization prescription for Cold Lake per se, but rather to illustrate how incorporating mechanism can influence how areas are prioritized to potentially have more immediate benefits to caribou. We also note that each prioritization approach could be extended to include PDs.

For each approach, we partitioned the Cold Lake range into approximately 10 × 10-km townships (or cells), which is a common geographic unit in Alberta. We then prioritized townships using data characterizing land cover, human footprint, and forest fires <40 years old (Alberta Biodiversity Monitoring Institute, 2019, 2021; Alberta Ministry of Agriculture, Forestry and Rural Economic Development, 2021). Following the federal recovery strategy (Environment and Climate Change Canada, 2020), we buffered the human footprint (LDs and PDs) by 500 m. We then selected conventional seismic lines (CSLs; >10 m wide, Dickie et al., 2017) as the target for restoration. For the GIU approach, we used the following equation to prioritize townships:

$$\mathrm{GIU} = \frac{\begin{array}{c}\%\ \text{area currently disturbed}\\ -\,\%\ \text{area disturbed in future (no CSLs)}\end{array}}{\text{CSL density in township}}.$$

Using seismic line density as a "cost" in the denominator, this equation places a higher priority on townships with low densities of seismic lines, which is also where buffered seismic lines are less likely to overlap (i.e., overlapping buffers increase cost per unit of undisturbed area gained). This approach therefore attempts to maximize undisturbed area gained per unit cost but is invariant as to where those undisturbed areas occur. In contrast, the GIR approach places a higher priority on maximizing undisturbed peatland area gained per unit cost:

$$\mathrm{GIR} = \frac{\begin{array}{c}\%\ \text{area currently disturbed in peatlands}\\ -\,\%\ \text{area disturbed in peatlands in future (no CSLs)}\end{array}}{\text{CSL density in township}}.$$

Prioritization scores were binned into five zones with each zone containing an equal number of townships (zone 1 = highest priority, zone 5 = lowest).

The two approaches produced different spatial patterns of prioritization (Figure 2). The GIU approach yielded higher priority for townships clustered on the eastern edge of the range. Conversely, the GIR approach placed a higher priority on townships located more centrally. The GIR approach also resulted in more connectedness among high-priority townships across the range, whereas the GIU approach resulted in a more spatially disjunct pattern with lower priority townships bisecting higher priority townships situated on the range's periphery. By creating larger intact patches of refugia for caribou, the GIR approach should provide greater and/or faster demographic benefits to caribou. Ultimately, this assumption should be tested empirically, though such testing requires large spatial scales and long timeframes. With conservation actions urgently needed for many caribou populations, we suggest that the absence of empirical testing should not preclude using a theoretical understanding of putative mechanisms of decline to inform prioritization approaches.

Given that all Alberta populations ($n = 11$) of boreal caribou are classified as not self-sustaining (Environment and Climate Change Canada, 2020) and the high costs of restoration (Johnson et al., 2019; Schneider et al., 2010), a second step to consider is prioritizing among ranges. At this scale, prioritization approaches often incorporate factors such as population status (e.g., size and trend) and access to natural resource reserves (Dickie et al., 2023; Schneider et al., 2011). We suggest that understanding current and emerging threats, in particular climate change, can also inform this process. Here, we consider climate change as a potential confounding effect on the future efficacy of habitat restoration, the conservation action that is the focus of our prioritization framework. This among-ranges step is not intended to address the mechanisms associated with climate change per se

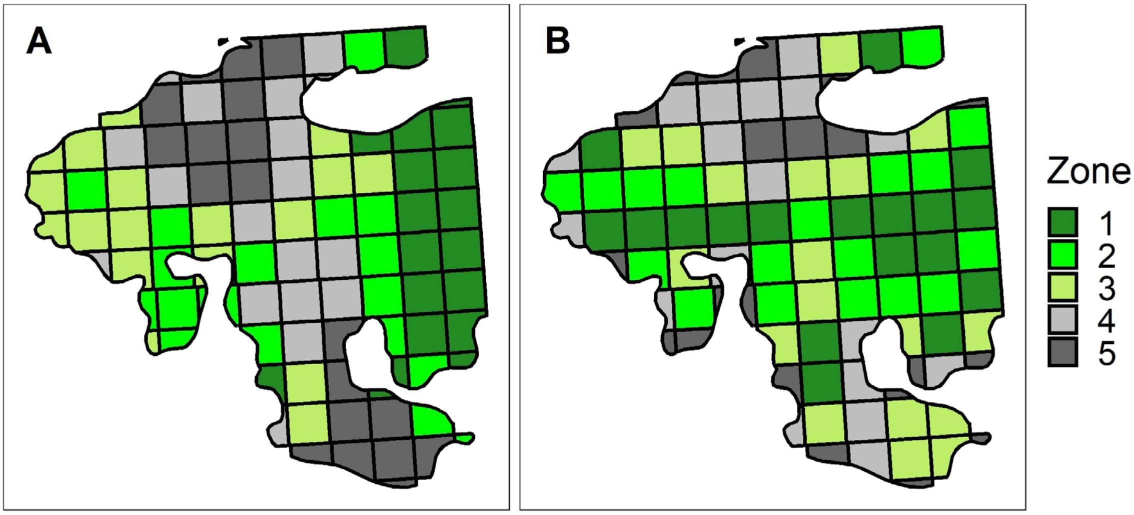

FIGURE 2 Prioritizing areas for restoration (zone 1 = highest priority, zone 5 = lowest) within the Cold Lake boreal caribou range. In the two approaches considered, the Cold Lake range is first partitioned into 10 × 10-km townships (squares). In the gain-in-undisturbed approach (A), prioritization maximized the gain in undisturbed area per unit cost but was invariant as to the type of land cover in which the disturbances occurred. In the gain-in-refugia approach (B), prioritization maximized the gain in undisturbed area occurring in peatlands per unit cost.

(Figure 1). Addressing climate-related mechanisms would require a different prioritization approach with potentially different objectives, such as targeting conservation actions toward the dominant climate mechanism in an effort to maintain the current distribution of caribou.

Prioritizing among caribou ranges presents a fundamental gamble because of the uncertainty associated with climate change combined with the current rate of habitat restoration. This gamble hinges on the idea that accelerating rates of climate change may prevent restored areas from becoming functional caribou habitat in the future. On one side of this gamble, higher priority could be placed on small and rapidly declining populations, which generally reside in ranges that are more southerly situated (Environment and Climate Change Canada, 2020; McFarlane et al., 2020). In Alberta, southern ranges are already being impacted by climate change (e.g., expansion of white-tailed deer, Dawe & Boutin, 2016; Latham, Latham, McCutchen, & Boutin, 2011), and accumulating evidence suggests that these ranges will transition out of systems conducive to self-sustaining caribou populations over the next 30–40 years (Baltzer et al., 2021; Barber et al., 2018; Deb et al., 2020; Rempel et al., 2021), a timeframe similarly required for restored areas to become functional caribou habitat. Focusing restoration on the "trailing edge" of caribou distribution may therefore yield low and diminishing returns in terms of conservation value for caribou (Gilbert et al., 2020). Such projections, however, are far from certain and an argument for prioritizing southern ranges is to provide these populations with high-quality habitat to maximize their potential resilience to climate change (Leblond et al., 2022; St-Laurent et al., 2022).

The other side of the gamble is to prioritize northern ranges where future climatic conditions (i.e., in the next 30–40 years) are predicted to still be conducive to self-sustaining caribou populations. Restoration would focus on this northern "core" and then move southward as conservation resources allow until restoration no longer becomes viable because of climate-induced landscape change. One criticism of this north-to-south approach is it seeks to maximize return on restoration investment at the apparent expense of southern populations. This strategy, however, does not suggest that existing protections be lifted for southern populations. Indeed, these populations may be supported by other management actions (e.g., predator control; Serrouya et al., 2019) if maintaining the current distribution of caribou is a management objective or as a hedge that climate change effects will be less severe than predicted.

Ultimately, the rate of habitat restoration will also factor into how ranges are prioritized. As an emerging field, technical advancements and continued improvement are needed to increase the rate and cost-efficiency of treatment deployment. As stated previously, habitat restoration is expensive with estimates varying from $100 million per range (Johnson et al., 2019) to several hundred million dollars across all Alberta ranges (Schneider et al., 2010). Currently, financial resources allocated to restoration are far below these estimates, resulting in most caribou ranges still incurring rates of habitat loss exceeding those of habitat gain (Nagy-Reis et al., 2021).

For example, in Alberta, provincial funding for caribou habitat restoration was ~$10 million in 2020–2021 (Government of Alberta, 2020), and in British Columbia, $8.5 million has been allocated over a three-year period (Government of British Columbia, 2020). To achieve habitat conditions conducive to the recovery of caribou populations, financial allocations to habitat restoration will need to increase by at least an order of magnitude and treatments need to be deployed over large spatial scales in a short timeframe. Moreover, achieving meaningful rates of habitat gain will also require concomitant habitat protection (i.e., habitat restoration should not be construed as a license to continue "business as usual" or rely on population management in perpetuity; Johnson et al., 2022; Serrouya et al., 2019). This urgency to gain habitat is particularly important for southern ranges as delays in treatment deployment will increase the likelihood that restored areas will be compromised by climate change before becoming functional caribou habitat.

For most caribou ranges, restoration costs are only a portion of the total realized costs. Habitat restoration and protection will reduce access to natural resource reserves, which in Alberta alone have estimated values in billions of dollars (Hebblewhite, 2017; Schneider et al., 2011). There is a distinct possibility that such costs may not be supported by governments and society, despite federal legislation mandating the protection of caribou critical habitat. For managers, such an outcome will likely necessitate conservation prioritization (Hebblewhite, 2017; Schneider et al., 2010), particularly if attaining self-sustaining status is still an objective for at least some populations. We suggest that for any such approach, climate change will need to be factored into how ranges are prioritized.

DISCUSSION

Understanding mechanisms driving population decline is fundamental to developing effective and efficient conservation strategies (Williams et al., 2020). Using the DPP as a guiding framework, we examined mechanisms linking ultimate causes of caribou population declines to their proximate demographic effects. We demonstrated that a mechanistic understanding can inform how areas are prioritized for conservation actions. Although it is unknown whether caribou populations will respond differently depending on the spatial deployment of habitat protection and restoration, we suggest that a mechanistically informed prioritization process has the potential for a higher "bang-for-the-conservation-buck" than one that does not. For boreal caribou and other similar species—that is, ones that are wide-ranging (e.g., Pacific salmon [*Oncorhynchus* spp.]; Barnas et al., 2015), prefer old-growth conditions (e.g., northern spotted owl [*Strix occidentalis caurina*]; Dunk et al., 2019), and/or reside in landscapes where restoration is logistically difficult and expensive—prioritization will be a necessary component of habitat-based conservation strategies.

In our prioritization example, we focused on mechanisms associated with landscape disturbance to prioritize conservation actions within caribou ranges and then considered projected impacts from climate change to prioritize among ranges. These two ultimate causes—landscape disturbance and climate change—present different challenges when developing mechanistically informed conservation strategies for boreal caribou and other species. For landscape disturbance, conservation actions addressing its primary mechanisms will also address its role as an ultimate cause of population decline, or to use a medical analogy, addressing the symptoms (mechanisms) can ultimately cure the disease (landscape disturbance). For climate change, local conservation actions will have little to no impact on its role as an ultimate driver of population decline. Nevertheless, if a management objective is to maintain the current distribution of a focal species, then understanding the dominant mechanisms associated with climate change, and targeting actions toward them, will increase the efficiency and effectiveness of conservation actions.

For boreal caribou, population declines are linked to landscape alteration and climate change by multiple mechanisms, though our review highlighted that some have more empirical and theoretical support than others (Table 1). The lack of empirical support made ranking the relative importance of mechanisms a difficult and, in some instances, subjective exercise. The lack of empirical evidence (i.e., linking a specific mechanism to an observed demographic outcome) was not unexpected given that mechanistic understandings are most often derived from experiments, and it is difficult to conduct such experiments on a low-density, wide-ranging species. However, the lack of empirical evidence should not be seen as an impediment to deploying conservation actions. Indeed, a large body of literature specific to boreal caribou has provided sufficient inferences to guide conservation actions (Boan et al., 2018), which is corroborated by our synthesis. Moreover, expanding our mechanistic understanding and enacting conservation strategies need not be mutually exclusive. Deploying actions in an adaptive management framework (e.g., Serrouya et al., 2019) can further test mechanisms of caribou population decline and subsequently improve the efficiency and effectiveness of conservation actions.

A fundamental challenge to stabilizing and recovering caribou populations is understanding their spatial requirements. As we identified, understanding the spatial scales over which apparent competition operates is a key knowledge gap. Currently, critical habitat is defined as the population's range (Environment Canada, 2008; Environment and Climate Change Canada, 2020), yet range sizes, as defined by current boundaries, can differ substantially. Range boundaries are primarily based on location data from radio-collared female caribou or expert knowledge (Environment Canada, 2012; Environment and Climate Change Canada, 2020). For some ranges, it may not have been clear as to whether populations were increasing, stable, or declining at the time of range delineation. It is well known that a species' distribution will contract during sustained declines (Brown, 1984); consequently, current boundaries may not reflect the spatial requirements for stable populations of caribou. Addressing this knowledge gap will require targeting treatments at specific ranges to restore large, contiguous areas and monitoring the demographic response of caribou. This type of approach is currently being used in the East Side Athabasca River and Cold Lake caribou ranges where collaborations among industry stakeholders are restoring LDs and monitoring the response of caribou, moose, and their predators (Dickie et al., 2021; RICC, 2020; Tattersall et al., 2020). Although prominent public commitments to restoration have been made (e.g., $32 million over 10 years; https://www.cbc.ca/news/canada/calgary/cenovus-caribou-32m-replanting-forests-seismic-1.3634134), to date, no project has yet attained scales similar to caribou ranges, and longer term monitoring (e.g., 10–30 years) will be required to better assess the efficacy of these restoration efforts.

We extended the framework of the DPP to include mechanisms associated with an emerging threat, climate change. In Canada's federal recovery strategy for boreal caribou (Environment and Climate Change Canada, 2020), climate change is considered a "medium" threat, ranking behind habitat alteration, and a recent retrospective analysis supports habitat alteration as a more important driver of current population declines than climate change (Neilson et al., 2022). Caro et al. (2022) also argued that climate change is still a secondary threat compared with habitat alteration for most species. Here, we placed an increased emphasis on climate change as a threat to boreal caribou for a number of reasons. First, many caribou populations reside in highly disturbed ranges that will take decades to recover to the older forest conditions necessary for population stability, and climate change may further delay or greatly alter the successional trajectory of vegetation communities (Taylor et al., 2020). During this time, climate change is predicted to accelerate (Smith et al., 2015), and although there is considerable uncertainty in the magnitude of climate-related effects, there is reasonably high certainty that these effects will be negative for boreal caribou. Second, while there may be uncertainty about the relative influence of habitat alteration and climate change on current declines of caribou, particularly among regions (e.g., western vs. eastern Canada), rates of habitat alteration can be addressed by local management actions, whereas rates of climate change cannot. Thus, as climate change progresses, the relative importance of climate change on caribou demography and distribution is likely to increase and, potentially, surpass that of habitat alteration (e.g., Barber et al., 2018; Leblond et al., 2022). Third, habitat-based conservation strategies for caribou have necessarily long timeframes (i.e., decades). Given this fact, failing to incorporate climate change predictions into conservation strategies will likely diminish their effectiveness in a long term. Finally, there may be an underappreciation of recent work suggesting that climate change may have an impact equal to or greater than landscape disturbance as a numerical driver of apparent competition, at least in western ranges of caribou (Dawe & Boutin, 2016; Fisher et al., 2020; Latham, Latham, McCutchen, & Boutin, 2011; Laurent et al., 2021).

We used boreal caribou as a case study because of the considerable challenges associated with their conservation (Hebblewhite, 2017). Yet, boreal caribou are not an isolated example, and other species face similar challenges. In western North America, habitat alteration of inland watersheds has contributed to widespread declines of Pacific salmon (*Oncorhynchus* spp.; Gregory & Bisson, 1997). Despite substantial investments in habitat restoration (e.g., >$100 million/year; Barnas et al., 2015), there is increasing recognition that prioritization may be necessary because of funding limitations and that restoring habitat for all populations is logistically infeasible, at least in the short timeframes required to prevent local extirpations (Walsh et al., 2020). Also, habitat restoration for salmon has thus far produced mixed results, partially due to restoration not always being targeted to the primary ecological need of the local population, prompting calls for a more mechanistic approach to restoration (Barnas et al., 2015; Walsh et al., 2020). A second example is greater sage-grouse (*Centrocercus urophasianus*), which have been declining due to the loss of mature sagebrush habitats (Walker et al., 2007). Restoring these habitats has been difficult because they may take >30 years to recover after disturbance (Baker, 2006). Restoration is also not straightforward because specific habitat requirements for sage-grouse vary by life history stage, and therefore nontargeted, broad-based restoration treatments have had limited success (Smith & Beck, 2018). These examples support our case study of boreal caribou, illustrating that for imperiled species residing in large landscapes where widespread habitat restoration is necessary, targeted restoration informed by a mechanistic understanding will be required to effectively and efficiently recover populations.

Finally, we acknowledge that for many species imperiled by habitat loss, the most pressing issue is achieving sufficient habitat protection and restoration to attain population stability, regardless of how these actions are deployed. For boreal caribou, the negative correlation between habitat disturbance and population growth rate has been known for over two decades (COSEWIC, 2002) and habitat protection and restoration have been key management recommendations in federal recovery strategies since 2011 (Environment Canada, 2012; Environment and Climate Change Canada, 2020). Yet, during this time, few caribou ranges have had habitat protected and/or restored at scales that could be reasonably expected to make a positive demographic impact on caribou (Environment and Climate Change Canada, 2017; Nagy-Reis et al., 2021). Reasons for the delay in habitat-based actions are likely complex and undoubtedly include socioeconomic factors (Fortin et al., 2020; Hebblewhite, 2017), but a broad-based objective of protecting and restoring habitat to a specified threshold (e.g., >65% undisturbed habitat; Environment and Climate Change Canada, 2020) may be daunting for managers overseeing ranges that are large in size and highly disturbed. We suggest that a mechanistic understanding of current and emerging threats to caribou may facilitate an increased deployment of habitat-based actions by informing how and where to begin.

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CONFLICT OF INTEREST STATEMENT

Three authors declare the following conflicts of interest: Thomas J. Habib is a biologist for Alberta-Pacific Forest Industries; Michael Cody is a biologist for Cenovus Energy Inc; and Amit Saxena was a biologist for Devon Canada Corp. and Canadian Natural Resources Limited. All listed companies are or were members of RICC.

DATA AVAILABILITY STATEMENT

Data were previously published and are available from publicly accessible data repositories (Alberta Biodiversity Monitoring Institute, 2019, 2021; Alberta Ministry of Agriculture, Forestry and Rural Economic Development, 2021).

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