# Mapping potential climate-change impacts on woodland caribou demographic rates

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## Executive Summary

Climate change is here and it is affecting ecosystems' composition, structure, and function in profound ways. This report details the possible impacts climate change may have on the population viability of woodland caribou (*Rangifer tarandus caribou*; mountain and boreal ecotypes; hereafter 'caribou'), a species that is already subject to local populations' declines and extirpations. After careful consideration of the scientific literature, we have decided to focus on six weather patterns that are shifting with climate change and that are expected to affect caribou vital rates: summer heat and length, drought, early spring onset, snow depth, winter severity, and ice-on-snow events. We chart the various pathways by which these six weather patterns, in addition to anthropogenic landscape disturbance, could impact caribou fecundity and survival. Climate change is expected to amplify existing deleterious processes impacting caribou population viability, and primarily unsustainable predation due to growing alternative prey populations. It is crucial to realize that deer and moose populations are very likely to keep growing and expanding under climate change. Our game harvest targets must be adjusted accordingly so that, at the very least, we are increasing sustainable yields, and, for the sake of caribou, we are suppressing primary-prey abundance. Further, we propose that sustaining caribou in the face of climate change would require a climatic-vulnerability assessment of each population's range to inform prioritization, followed by intensive habitat protection and restoration, and, where and when needed, predator control.

## Introduction

This report explores the potential pathways through which climate change can impact the demographic rates of caribou, both positively and negatively. A specific focus is given to distinguishing possible impacts of long-term radical habitat transformations (shifting from one distinct climax vegetation community to another) from short-term shifts in weather patterns. Climate change may impact caribou in a variety of ways, and these may interact with human-created landscape disturbances (e.g., forestry) to contribute to caribou population decline. Effective conservation and management of caribou populations in the face of climate change critically depends on understanding the various climate-impact pathways so that caribou recovery actions and strategies are developed accordingly. This report summarises the findings of a research project commissioned to Biodiversity Pathways by the British Columbia (BC) provincial government (under an SCA). The results of this project will help BC incorporate the effects of climate change into future management recovery actions for caribou. The stated goals of this project were:

1. Identify important pathways of climate change impacts to caribou.
2. Identify and use climate change projection data and tools to assess potential impacts of climate change on caribou and develop adaptation recommendations.
3. Develop research questions to address priority climate change pathway knowledge gaps.

In this report, we will address goals 1 and 3.

## Caribou demography

For the sake of brevity and clarity, we focus our report on the potential impacts climate change may have on three female caribou demographic rates: fecundity, calf survival, and adult survival. We acknowledge that caribou populations are comprised of more refined age classes (subadults and senescing; both with reduced fecundity and survival compared to prime-age adults), but these age classes are typically indistinguishable from adults and subadult males in the field, without excessive harassment. We also acknowledge that male caribou may be subject to slightly different constraints on their survival and fecundity than female caribou (particularly in harvested populations), but for the most part, a focus on the female part of the population is sufficient to capture and understand demographic trends.

## Climate change

There is ample evidence that climate conditions across many caribou ranges have significantly shifted over recent decades, and climate projections suggest conditions will continue change in the future (Almazroui et al., 2021; Brun et al., 2022; Li et al., 2019; Parisien et al., 2023; Rees et al., 2020; Wotherspoon et al., 2023; Yang et al., 2021; Zhao et al., 2020) (https://services.pacificclimate.org/plan2adapt/app/). Average temperatures, the annual number of growing degree days, and the frequency and magnitude of extreme-high temperature events are all on the rise and are expected to continue increasing at least until the end of the century. Moreover, the frequency of high-intensity precipitation events is increasing, while average spring and summer precipitation is decreasing (resulting in increasing drought conditions), and both trends are expected to persist. These trends are associated with heightened natural disturbance (wildfire and forest-pest outbreaks) frequency and severity (Bentz et al., 2021; Ellis et al., 2022; Fettig et al., 2022; Halofsky et al., 2020; Jain et al., 2022; Jones et al., 2022; Massey et al., 2023; Parisien et al., 2023; Sambaraju et al., 2019; Whitman et al., 2022), but also reduced post-disturbance regeneration (or increased recovery time) of several habitat-defining species (Boucher et al., 2020; D'Orangeville et al., 2023; Whitman et al., 2019). It should be noted that, in the absence of disturbance, vegetation communities may persist for many years outside of the respective climatic conditions to which they are adapted ('ecological inertia' (D'Orangeville et al., 2023; Holsinger et al., 2019; Stralberg et al., 2020). More uncertainty exists regarding trends in snow depth and the frequency of ice-over-snow events, although there are some indications that the former is decreasing whereas the latter might be increasing (Bieniek et al., 2018; Groisman et al., 2016; Neupane, 2019; Pan et al., 2018; Wotherspoon et al., 2023). Overall, climate change is no longer a possibility – it is a reality that caribou conservation must acknowledge and adapt to.

## Distinguishing climate change from habitat change

Numerous studies aim to either forecast or hindcast wildlife distribution (and sometimes even abundance) under climate change, and several of these studies focus exclusively on caribou (Barber et al., 2018; Cadieux et al., 2020; Labadie et al., 2023; Leblond et al., 2022; Masood et al., 2017; Morineau et al., 2023; Neilson et al., 2022; Rempel et al., 2021; Stewart et al., 2023; Stoklosa et al., 2015). Most of these studies, however, rely solely on the observed statistical relationship between species occurrence or abundance patterns and their associated climatic envelopes and/or habitats (qualitatively distinct vegetation communities). Indeed, almost all published research about the effects of climate change on caribou assumes, explicitly or implicitly, habitat (or climatic-envelope) transformation as the sole driver of change (but see (DeMars et al., 2021, 2023; Neilson et al., 2022; Schmelzer et al., 2020)).

Climate change is associated with significant shifts in weather patterns and these shifts can have various (and even contrasting) effects on caribou demographic rates (Canonne et al., 2023). The effects of shifting weather patterns on caribou demographic rates could unfold quickly (within years or even months) but be relatively ephemeral (DeMars et al., 2021, 2023; Schmelzer et al., 2020), or, when operating via radical habitat transformation, could take decades to unfold but be long lasting. The distinction between the impacts of long-term habitat transformation and short-term shifts in weather patterns is important for two reasons. First, it helps formulate mechanistic hypotheses and predictions and aid in communication among researchers and policymakers. Even more important though, climate-change-induced habitat transformations are slow and unpredictable because they are often triggered by stochastic disturbance events such as wildfire and insect outbreaks. Because boreal and alpine vegetation communities are characterized by slow life histories, caribou habitat may persist for decades (in the absence of a triggering disturbance event) while outside of its apex climatic envelope. Our understanding of climate change impacts on caribou, as well as any mitigation strategy, thus depends on teasing apart habitat-mediated effects from other, more immediate and predictable, environmental changes.

## The Six Culprits

After review of the scientific literature (e.g., (DeMars et al., 2021, 2023; Morineau et al., 2023; Schmelzer et al., 2020; Stewart et al., 2023; Tyler, 2010), we have identified six weather patterns that are either shifting, or are expected to shift with climate change, and that may have substantial effects on caribou population health (Figure 1; see below for further details about each of these weather patterns):

1. Summer heat and length
2. Drought
3. Timing of spring green-up
4. Snow depth
5. Winter severity
6. Ice-on-snow events

Below we review the possible causal chains of effects for each one of these patterns, in addition to the impacts of the seventh driver: anthropogenic disturbance.

Because of the complexity of the problem at hand (DeMars et al., 2023), we opted to use Directed Acyclic Graphs (DAGs) to map the relationship between instrumental variables (climate change and anthropogenic disturbance), exposure variables (e.g., predator or resource abundance), and caribou vital rates (Wilson et al., 2021). DAGs are causal diagrams that are used to identify which causal effects can be determined based on observational data (Arif & Macneil, 2022; Arif & MacNeil, 2022; Larsen et al., 2019; Laubach et al., 2021). DAGs can thus help us define what data are required to support or refute a specific causal pathway, and thus prioritize knowledge acquisition (Wilson et al., 2021).

## 1. Summer heat and Length (Figure 1)

BC summers are becoming hotter and longer. This includes an increase in growing-degree days as well as an increase in average daily maximum temperature. These increases are expected to lead (everything else being equal) to a significant increase in primary productivity, dominated primarily by fast-growing (herbaceous or woody-deciduous) vascular plants, capable of using the increased availability of energy (light and heat) to build biomass. Primary consumers (herbivores), from ants and termites to moose and caribou, will benefit from this increase in primary production. Arthropods will moreover benefit directly from an increase in frequency and duration of activity-enabling thermal conditions (*i.e.* when it is physiologically hot enough). In addition, longer summers may also allow some arthropods to increase the annual number of reproductive cycles (generations), resulting in a substantial increase in cumulative arthropod biomass.

**1.1) Radical Habitat Transformation.** Hotter and longer summers will eventually lead to long-lasting and radical changes in vegetation-community (habitat) composition. As noted above, arthropods are expected to benefit from the increased flux of thermal energy, and this includes species that are considered forest pests, such as mountain pine beetle (*Dendroctonus ponderosae*). Increased productivity and volatility of forest pests lead to an increased likelihood of extensive stand-replacing pest outbreaks (Bentz et al., 2021; Fettig et al., 2022; Sambaraju et al., 2019). Moreover, hotter and longer summers result in more frequent, severe, and extensive stand-replacing forest fires (Ellis et al., 2022; Jain et al., 2022; Jones et al., 2022; Parisien et al., 2023; Whitman et al., 2022; Wotherspoon et al., 2023). Note that, whereas fire should have a negative effect on forest-pest outbreaks (dead trees are of no use to pests), pest-killed trees may be more susceptible to fire, although this synergism is still up to debate (Romualdi et al., 2023; Talucci et al., 2022). Hotter and longer summers may further result in reduced post-disturbance regeneration (or increased recovery time) of several habitat-defining species (Boucher et al., 2020; Brecka et al., 2020; Day et al., 2020; D'Orangeville et al., 2023; Guz et al., 2021; Jorgensen et al., 2023; Molina et al., 2022; Seidl & Turner, 2022; Stevens-Rumann et al., 2022; White et al., 2022; Whitman et al., 2019).

Once mature trees (currently dominated by slow-growing coniferous species in caribou ranges) are killed by either fire or pests, they will be replaced by species better adapted to the changing climate and frequent disturbances, with increased dominance of deciduous tree species, shrubs, and grasses (Brecka et al., 2020; Day et al., 2020; Jorgensen et al., 2023; Massey et al., 2023; Molina et al., 2022; Seidl & Turner, 2022; Stevens-Rumann et al., 2022; Whitman et al., 2019). Unlike the ephemeral shift in primary productivity described above, stand-replacing disturbance events, in combination with climate-change effects on post-disturbance successional trajectories, will result in lasting radical shifts from one qualitatively distinct vegetation community to another (either 'reassembly' or 'replacement' sensu (Seidl & Turner, 2022)). Such habitat transformations will lead to substantial 'habitat-mediated effects' on caribou vital rates, many of which driven by the associated long-term increase in vascular-plant productivity (Labadie et al., 2021; Neilson et al., 2022; Serrouya et al., 2021). It should be noted however that an increase in vascular-plant productivity does not necessarily mean negative outcomes for caribou – specific pathways need to be outlined and evaluated to assess the net impact (see next sections).

**1.2) Micropredation.** The expected increase in the abundance of arthropods includes species that feed on live mammalian tissue (micropredators). Caribou are known to be sensitive to insect harassment and both their movements and habitat selection are influenced by the local abundance of mosquitos and several biting or parasitic fly species (Handeland et al., 2021). Whereas it is possible that intense enough micropredation (by biting insects or parasitic larva) carries direct fitness costs, it is more likely that insect harassment carries indirect costs by forcing caribou to spend time avoiding it rather than foraging or hiding from predators (Cook et al., 2021; Denryter et al., 2022; Ion & Kershaw, 1989; Raponi et al., 2018). A significant increase in the cumulative abundance of biting insects will thus likely translate to a significant impact on caribou body condition (somatic growth, fat reserves, nutrient deficiencies, etc.).

**1.3) Predation.** Increased biomass of primary consumers leads to increased biomass at higher trophic levels (Serrouya et al., 2021), including several species that predate on caribou:

- Black bears (*Ursus americanus*) and coyotes (*Canis latrans*). Both species will not only benefit from increased abundance of their primary prey (including, in the case of black bears, arthropods such as ants), but also benefit directly from increased primary production, as both species rely on plant-rich diets. Both species are thought to predate primarily on young calves, and are thus expected to have little impact on adult survival, but may significantly impact neonate survival.
- Golden eagles (*Aquila chrysaetos*). Eagles are known to occasionally predate on mountain caribou neonates. Eagle populations have been on the rise in recent decades, and likely benefit from increased biomass of their primary prey species (lagomorphs and rodents).
- Wolves (*Canis lupus*), cougars (*Puma concolor*), wolverines (*Gulo gulo*), and Grizzly bears (*Ursus arctos horribilis*). These species are all expected to benefit from increased biomass of their primary prey species (deer, moose, and elk). Grizzly bears will also benefit directly from increased primary production (Grizzly bears are obligate carnivores but a substantial portion of their calorie intake comes from berries and other plant material). Increased population sizes of these large carnivores may lead to increased incidental predation on caribou (secondary prey), both calves and adults. Note that in some systems, caribou may be the primary prey of wolves (Merkle et al., 2017) and may thus be less prone to increased wolf predation due to increasing deer and moose populations.

Note that, based on our current understanding of caribou ecology, these predators are not expected to have equivalent impacts on caribou population viability. For adult caribou, wolves are by far the most important predators, likely followed by the more narrowly distributed cougars and Grizzly bears, and the substantially less abundant wolverines (but note that in some systems black bears are also known to predate on adult caribou; (Bonin et al., 2023; Stotyn, 2008)). For neonates, bears, coyotes, and wolverines are known to be important predators. Furthermore, Grizzly bears are competitively dominant over wolves but are only active during the summer months (and even then, are likely not actively hunting past spring). Wolves are competitively dominant over cougars, and may even predate on wolverines, black bears, and coyotes. Hence, an increasing abundance of wolves may depress the abundance of other carnivores, whereas an increasing abundance of black bears may actually subsidize a growing wolf population (Martins et al., 2020; Tallian et al., 2022) .

In summary, an important outcome of hotter and longer summers is increased vascular-plant productivity, resulting in increased large-herbivore abundance, and subsequent increased predator abundance, which ultimately results in increased spatial overlap between predators and caribou. This increased spatial overlap may have impacts on both adult and calf caribou survival that far exceed the impacts of predator abundance alone. Caribou have evolved to rely on large-scale spatial separation from their predators and their predators' primary prey. An expansion of predators into core caribou habitat nullifies the effectiveness of this antipredation strategy, resulting in decreased survival across all age classes.

**1.4) Pathogens and parasites.** Pathogen and parasite loads are expected to increase with exposure to alternative hosts (primarily other cervids, such as moose, elk, and deer), but also with the abundance of micropredators and ticks that serve as transmission vectors. As with the effects of micropredation, the most likely immediate impact of increased loads of parasites and disease is a reduction in caribou body condition (Handeland et al., 2021; Hughes et al., 2009). From the little known about the role played by pathogens and parasites in caribou population limitation, it is potentially a substantial one (Bondo et al., 2019; Dickinson et al., 2023; Koltz et al., 2022; Tryland & Kutz, 2018).

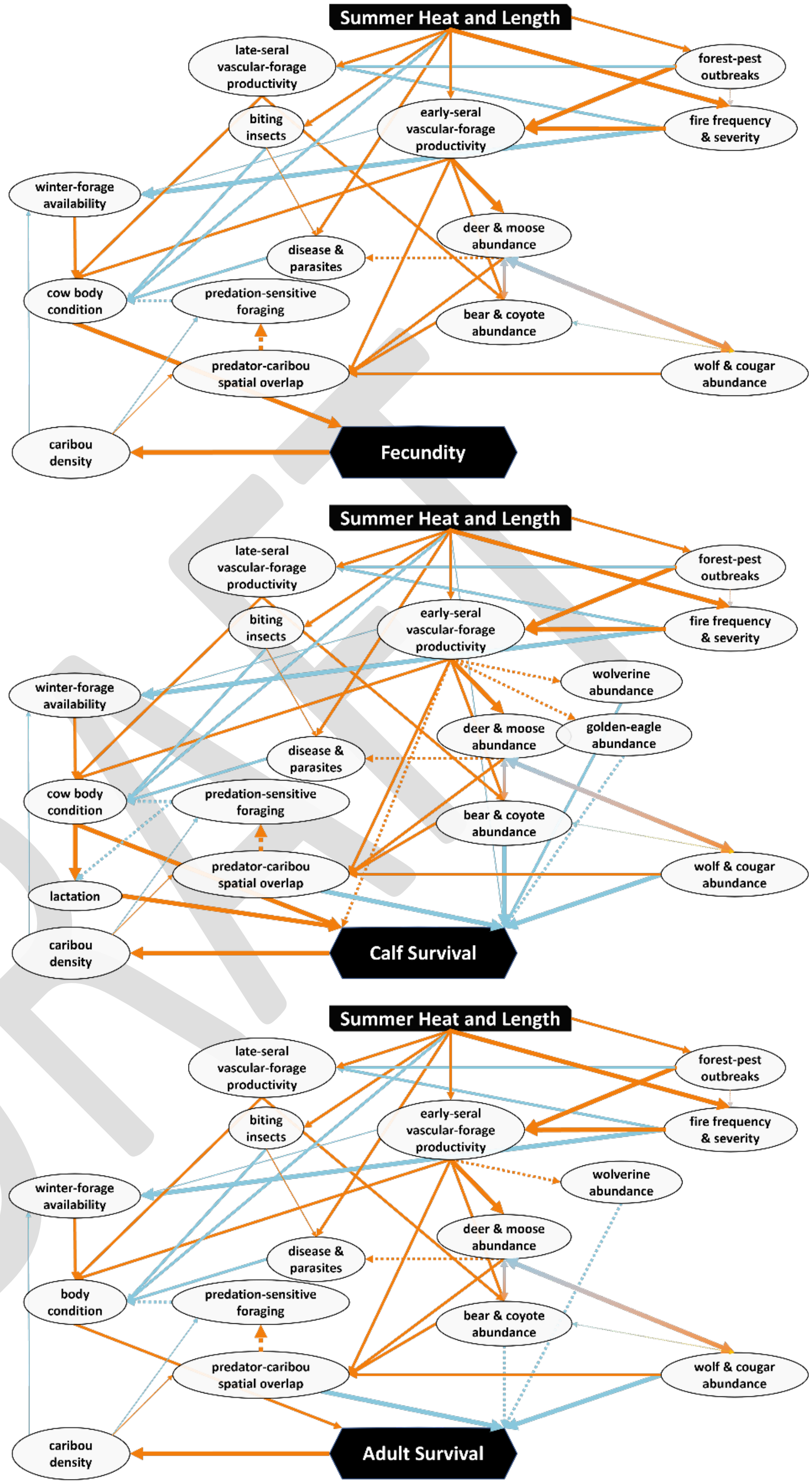
**1.5) Heat stress**. Caribou is a cold-adapted species, and their capacity to thermoregulate when facing heat stress is likely limited (although we know surprisingly little about this topic). Long hot summer days may carry significant physiological costs for caribou, both directly by causing heat stress, and indirectly through time spent in thermal refugia rather than in prime foraging habitats or predator refugia. Both mechanisms could reduce body condition.

**1.6) Winter forage availability.** Caribou forage on vascular woody forage in early winter but they quickly shift to rely almost exclusively on lichen as the season progresses. Caribou access ground lichen by cratering in the snow or foraging on wind-scoured slopes. Caribou access arboreal lichen from fallen snags, litter on top of the snow, and, where and when the snow gets deep enough, directly from standing trees (see 4.1 below). Lichen is associated primarily with mature coniferous stands, and is typically absent in post-disturbance regenerating stands where the understory is dominated by graminoids and the canopy by deciduous species. Post-fire lichen recovery time ranges between 30 and 75 years (Greuel et al., 2021). Note however that disturbance impacting only the canopy but not the forest floor, such as forest-pest outbreaks, may temporarily enhance terrestrial lichen productivity on the forest floor. Overall, increased vascular plant productivity is expected to be associated with decreased lichen biomass.

Lichen is generally a poor source of protein (2-10% crude protein) and is instead rich primarily in hemicellulose (60-80%). This, combined with its low digestibility (30-40% in caribou rumen fluids), suggests that caribou may be nutritionally limited during winter. If that is the case, reduced lichen abundance and distribution could lead to increased overwinter mortality, either directly from starvation or indirectly due to predation of weakened individuals. Increased mortality may be expected to be particularly evident in sections of the population entering winter in relatively poor body condition, i.e., calves, post-rut bulls, and lactating or senescing cows. We note however that this pathway lacks empirical support (McLellan et al., 2012). Further, data suggest that, across years and ecotypes, adult caribou body condition is maintained to an exceptional degree through the winter (Cook et al., 2021). Still, we cannot rule out the possibility that reduced lichen abundance could result in decreased fecundity (fetus absorption or abortion due to insufficient energy and protein supply), reduced calf survival in the subsequent year (due to small neonate body size and poor milk quality of nutritionally stressed cows), and reduced pregnancy rates in the following winter ('carry-over' effect).

**1.7) Non-lichen forage availability.** During the snow-free season, caribou diet is much broader than their winter diet, including vascular plants (primarily deciduous shrubs and herbaceous vegetation), in addition to lichen and fungi. Compared to their winter diet, this diet is much richer in digestible protein and carbohydrates, but the nutritional demands during the snow-free season are also higher. Heat stress and insect harassment may limit the time available for animals to forage, and lactating cows require a tremendous amount of energy and protein to nourish themselves and their calves. Calf mortality is a function of calf nutrition, which critically depends on lactating cows having access to nutritious forage. Other ungulates are known to be particularly sensitive to forage limitations during the fall (when animals need to put on fat reserves to help them through the winter, vegetation senesces, and rut may add additional energetic costs). Evidence that such is the case in caribou are mixed, but there are some indications that caribou are forage-limited during the snow-free season (Cook et al., 2021; Denryter et al., 2022). An increase in the abundance and distribution of vascular forage species may thus have a positive effect on caribou population health (everything else being equal), but the potential magnitude of this effect is currently unknown.

**Figure 1 – DAG representation of the various hypothetical pathways that may lead from an increase in summer heat and length to increased fecundity, juvenile survival, and adult survival. Orange arrows indicate that an increase at their start-node leads to an increase at their end-node (positive effects). Pale-blue arrows indicate that an increase at their start-node leads to a decrease at their end-node (negative effects). Double-headed arrows represent bidirectional effects, and dashed arrows reflect qualitatively questionable effects. Arrow thickness reflects a qualitative ranking of expected effect size: large (thick), medium, or small (thin).**



## 2. Drought (Figure 2)

Drought is the deficiency of precipitation over an extended period of time. In the context of caribou ranges, drought conditions are born out of reduced snow accumulation during winter followed by reduced rainfall during the spring and summer. Drought conditions are expected to become more severe, and last longer, under climate change.

Drought conditions generally reduce vascular-plant productivity and may hence slow down short-term shifts in the vegetation community (benefiting caribou), but also (**2.1**) reduce non-lichen forage availability and quality (negatively impacting caribou body condition; see also 1.7). More importantly, drought conditions are associated with an increased risk of stand-replacing forest fires, and make trees more susceptible to insect attacks, thus increasing the likelihood of forest-pest outbreaks. Overall, (**2.2**) droughts are much more likely to accelerate the process of radical habitat transformation from low-productivity (at least in terms of vascular forage) coniferous forests to high-productivity (but low-lichen) mixedwood, shrubland, or savannah ecosystems (see also 1.1). As such, droughts are expected to have a net negative impact on caribou populations.

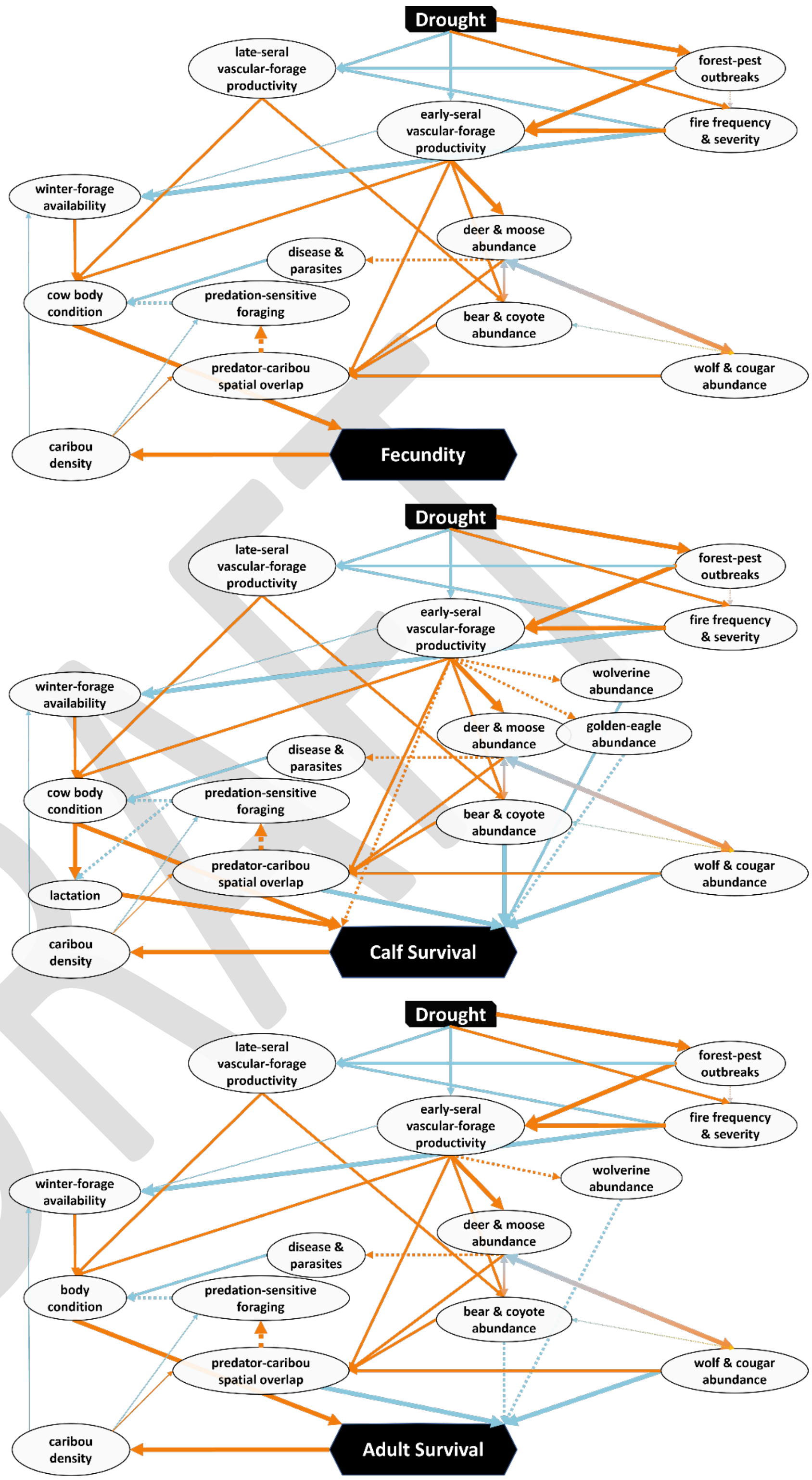



**Figure 2 - DAG representation of the various hypothetical pathways that may lead from an increase in the frequency and duration of drought events to increased fecundity, juvenile survival, and adult survival. Orange arrows indicate that an increase at their start-node leads to an increase at their end-node (positive effects). Cyanic arrows indicate that an increase at their start-node leads to a decrease at their end-node (negative effects). Double-headed arrows represent bidirectional effects, and dashed arrows reflect qualitatively questionable effects. Arrow thickness reflects a qualitative ranking of expected effect size: large (thick), medium, or small (thin).**

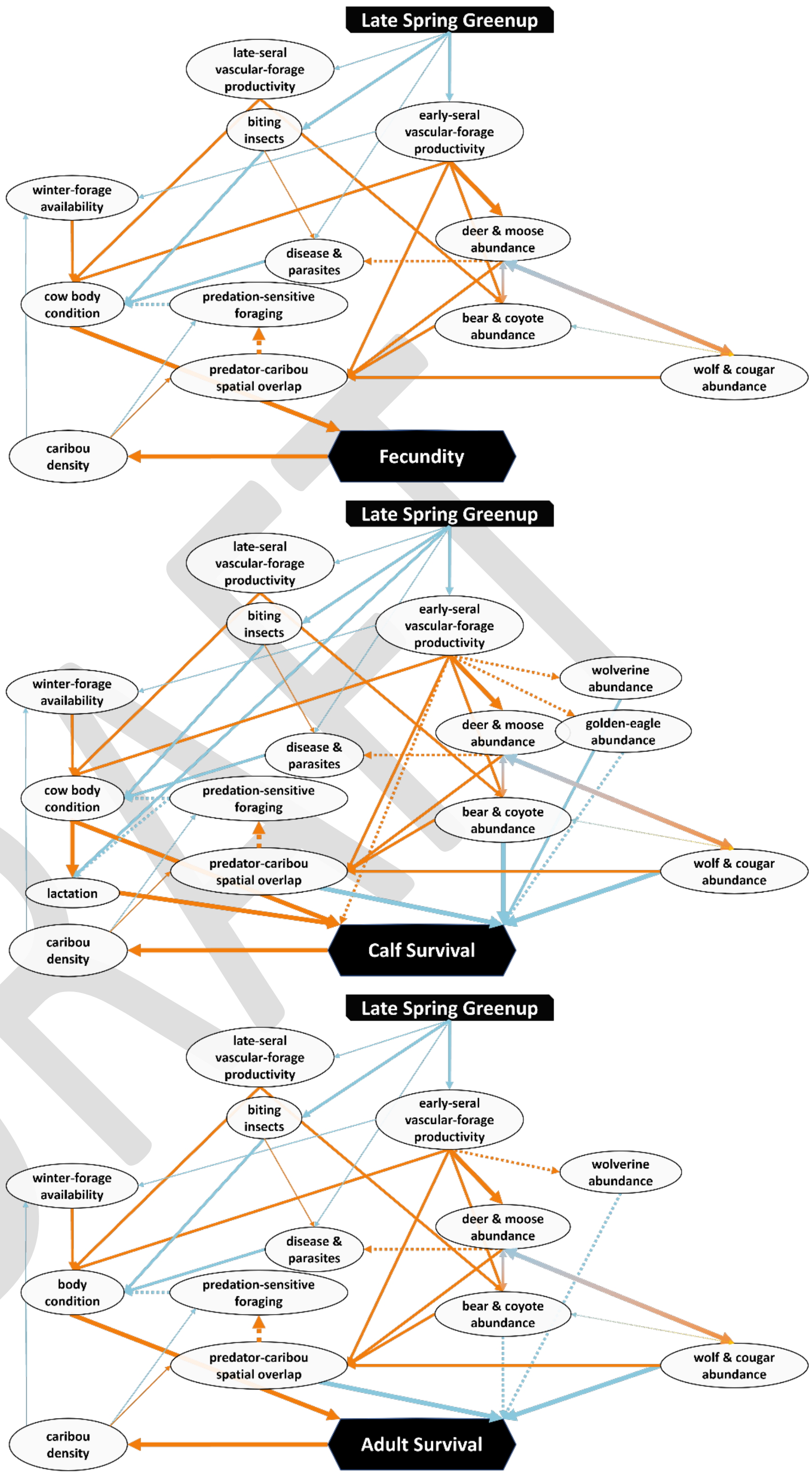
## 3. Timing of Spring Green-up (Figure 3)

The timing of spring green-up (the onset of the growing season) varies across space and time as a function of spring precipitation and temperature. Overall, climate change is expected to drive a trend of earlier spring green-up across most of the boreal. However, the increased frequency and severity of spring snowstorms would translate to low predictability of spring green-up timing.

**3.1) Lactation.** Vascular forage nutrient and protein digestibility peaks midway through spring green-up – that is when newly emerging stems and leaves are still poor in defensive and structural compounds (typically when the rate of plant-biomass accumulation is highest, rather than when biomass itself peaks later in the summer). Lactating caribou cows, as many other herbivores, rely on nutrient-rich forage to fuel their heightened energy and protein needs and their lactation performance is thus tightly linked with spring green-up. Caribou gestation time is fixed, resulting in a narrow parturition pulse (typically in late May). Therefore, any mismatch between caribou parturition and spring green-up (due to climate-change-driven shifts in the timing of spring green-up) could lead to nutrient deficiency during the period lactating cows need it most, resulting in poor lactation and hence poor calf survival.

**3.2) Micropredation.** Spring green-up marks the first emergence of overwintering arthropods, including biting insects and ticks. Early spring leads to early emergence, which could result in an additional breeding cycle, substantially increasing the cumulative impacts these micropredators could have on caribou body condition (see also 1.2 and 1.4).

**Figure 3 - DAG representation of the various hypothetical pathways that may lead from a shift to late spring green-up to increased fecundity, juvenile survival, and adult survival. Orange arrows indicate that an increase at their start-node leads to an increase at their end-node (positive effects). Cyanic arrows indicate that an increase at their start-node leads to a decrease at their end-node (negative effects). Double-headed arrows represent bidirectional effects, and dashed arrows reflect qualitatively questionable effects. Arrow thickness reflects a qualitative ranking of expected effect size: large (thick), medium, or small (thin).**



## 4. Snow Depth (Figure 4)

Snow is a defining feature of caribou ranges during winter. Snow depth varies substantially through space and time, and current climate change projections indicate that this variability is expected to increase. As to the mean snow depth, it may increase as a result of increased winter precipitation driven by an increase in air humidity due to increasing temperatures, but it could also decrease due to frequent thawing events, denser (wetter) snow, and shorter winters. Whereas there are uncertainties about the expected trends of snow depth within caribou ranges under climate change, most studies predict a significant decrease in mean snow depth accompanied by increased variability across space and time (Islam et al., 2017; Mortezapour et al., 2022; B. W. Newton et al., 2021; Schnorbus et al., 2014; Sobie & Murdock, 2022) (https://services.pacificclimate.org/plan2adapt/app/).

**4.1) Winter forage availability.** As detailed above, caribou rely heavily on lichen during winter but ecotypes differ substantially as to how they do this. Boreal woodland caribou access ground lichen by digging (cratering) through the snow. Whereas they are highly adapted to this foraging strategy (they can smell lichen through the snow and efficiently uncover it with their hoofs and snouts), the deeper the snow the more costly this foraging strategy is, and it is possible that very deep snow prohibits effective cratering all together. Hence, deep snow may be associated with winter forage limitation in boreal woodland caribou. Most Mountain caribou populations also rely on ground lichen, but their main access strategy is to feed on windswept slopes where snow depth is much less of a barrier. That said, it is (although heavy and frequent snowfall likely impacts the availability of such snow-free areas; (Holtan et al., 2023)). On the other hand, the southern group of Southern Mountain caribou (COSEWIC's DU9) rely primarily on arboreal lichen which they are able to reach due to the exceptionally high snowpack characterizing their ranges, the same snowpack that suppresses lichen growth closer to the ground. Consequently, at the onset and at the end of the winter season, or during low snowpack years, DU9 caribou cannot access their prime food source and are hence forced to migrate down to lower elevations where they feed on evergreen shrubs (primarily *Paxistima myrsinites*) and arboreal lichen litterfall (Kinley et al., 2007). Coincidently, these lower elevation ranges as well as some of the migratory routes that lead to them are heavily anthropogenically disturbed, which might explain why 30% of this ecotype's subpopulations are now functionally extirpated. Lastly, it should be also noted that for all ecotypes, deep snow may inhibit access to vascular forage early in the winter, but the relative significance of this limitation is unknown.

**4.2) Predation.** Snow depth could affect the predation of caribou via two distinct pathways (Horne et al., 2019; Olson et al., 2021; Sullender et al., 2023). First, predators, and particularly wolves, travel less in deep snow. This means that, when snow is deep, wolves are less likely to venture into caribou habitat (effectively reducing their spatial overlap with caribou), and are less likely to encounter prey in general due to reduced search rate (the rate at which the predator scans new area). This latter effect may also translate into a numerical response of the wolf population – a reduced search rate will, in the long term, result in reduced cumulative prey intake and hence reduced wolf abundance. In other words, deep snow makes wolves less efficient predators. However, primary prey species that are less adapted to movement through deep snow (e.g., deer, elk, and bison) may become more vulnerable to wolf predation as snow gets deeper, and are more prone to malnutrition due to the cost of thermoregulation and inability to access food resources. Deer in particular are not adapted to movement and foraging in deep snow, and are thus prone to winter starvation (or compensatory predation) in deep-snow winters (Clare et al., 2023; LaSharr et al., 2023; Laurent et al., 2021; Norton et al., 2021). Therefore, the second pathway through which snow depth might affect predation is that prolonged periods of deep snow are expected to greatly reduce primary-prey population size. Predator abundance is tightly linked to primary-prey abundance, meaning that deeper snow is expected to benefit caribou by reducing predator-caused mortalities across all age classes.

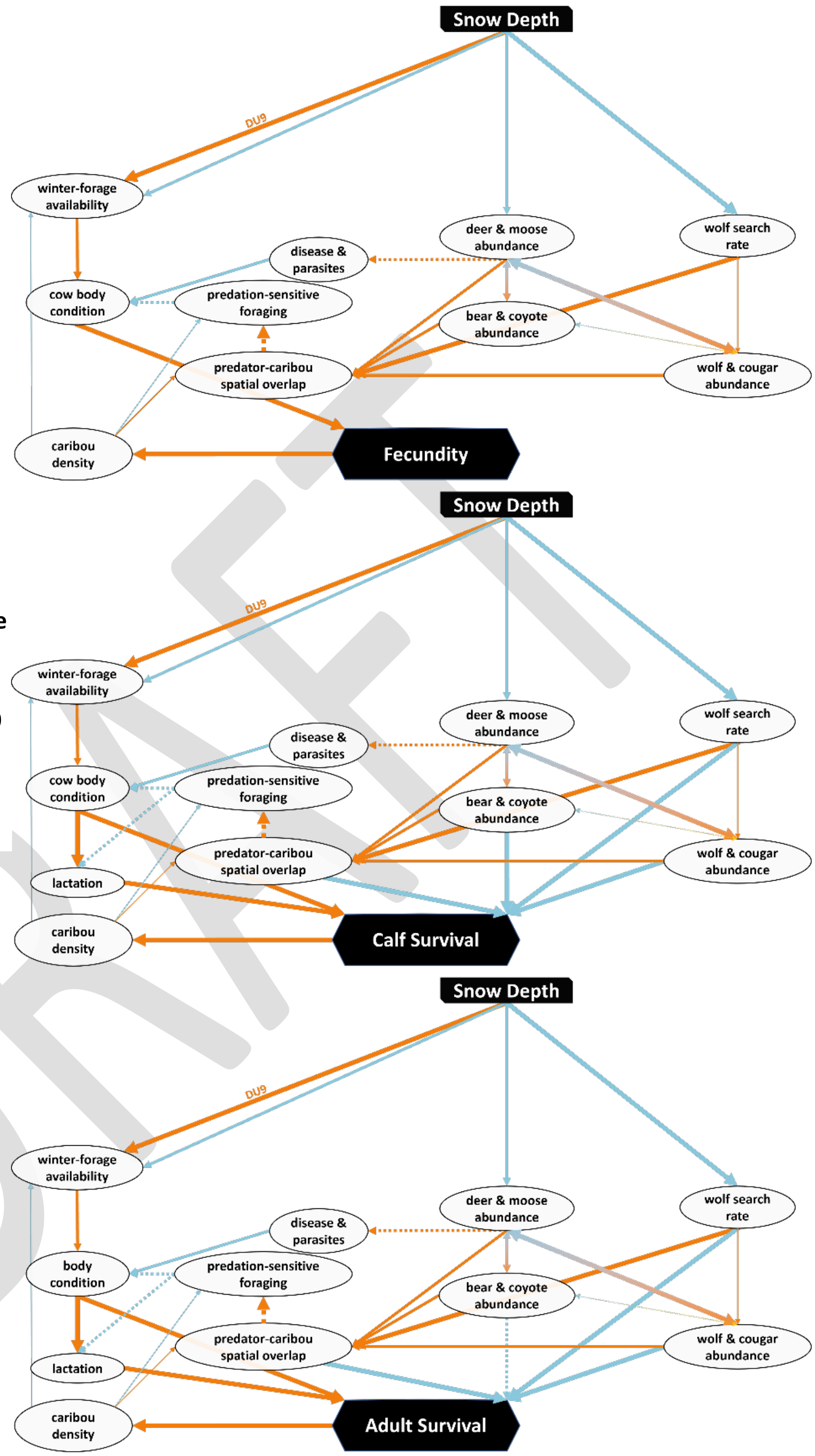



**Figure 4 - DAG representation of the various hypothetical pathways that may lead from an increase in snow depth to increased fecundity, juvenile survival, and adult survival. Orange arrows indicate that an increase at their start-node leads to an increase at their end-node (positive effects). Cyanic arrows indicate that an increase at their start-node leads to a decrease at their end-node (negative effects). Double-headed arrows represent bidirectional effects, and dashed arrows reflect qualitatively questionable effects. Arrow thickness reflects a qualitative ranking of expected effect size: large (thick), medium, or small (thin). Note the separate arrows indicating a strong positive effect of snow depth on winter-forage availability for DU9 caribou (the southern group of Southern Mountain caribou; see 4.1 for details)**

## 5. Winter Severity (Figure 5)

Winter severity is typically measured as a cumulative non-linear function of daily or hourly temperature (e.g., the number of days that had temperature maxima less than -20°C). Winter severity is expected to decrease with climate change.

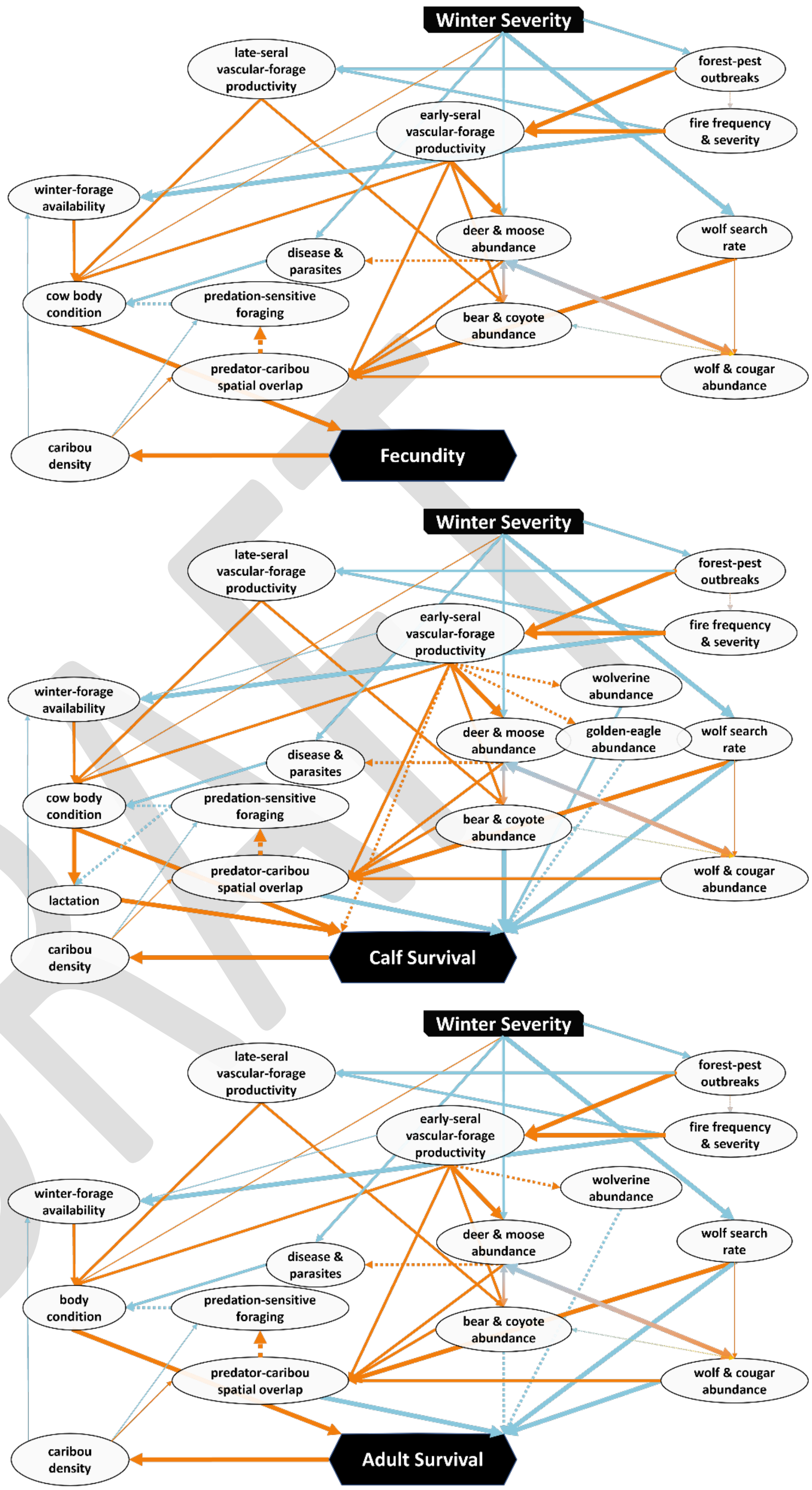
**5.1) Habitat change.** Milder winters are associated with increased overwinter survival of forest pests, leading to forest-pest outbreaks (endemic species becoming epidemic) and hence radical habitat transformation (see also 1.1).

**5.2) Micropredation and disease.** Milder winters are associated with increased overwinter survival of biting insects and ticks, leading to increased micropredation pressure on caribou, as well as a potential increase in disease transmission due to increased vector (ticks and mosquitoes) abundance (see also 1.2 and 1.4).

**5.3) Predation.** Milder winters also mean growing and expanding primary-prey populations, supporting growing and expanding predator populations (see 1.3). White-tailed deer (*Odocoileus virginianus*) in particular is an expanding primary-prey species known to be strongly limited by winter severity, and hence expected to proliferate as winters become milder (Laurent et al., 2021).

**5.4) Heat stress**. Once in their winter coat, caribou are extremely thermally insulated, making them prone to physiological heat stress during winter even more so than in summer (see 1.5). Mild winters may thus be energetically taxing for caribou.

**Figure 5 - DAG representation of the various hypothetical pathways that may lead from an increase in winter severity to increased fecundity, juvenile survival, and adult survival. Orange arrows indicate that an increase at their start-node leads to an increase at their end-node (positive effects). Cyanic arrows indicate that an increase at their start-node leads to a decrease at their end-node (negative effects). Double-headed arrows represent bidirectional effects, and dashed arrows reflect qualitatively questionable effects. Arrow thickness reflects a qualitative ranking of expected effect size: large (thick), medium, or small (thin).**



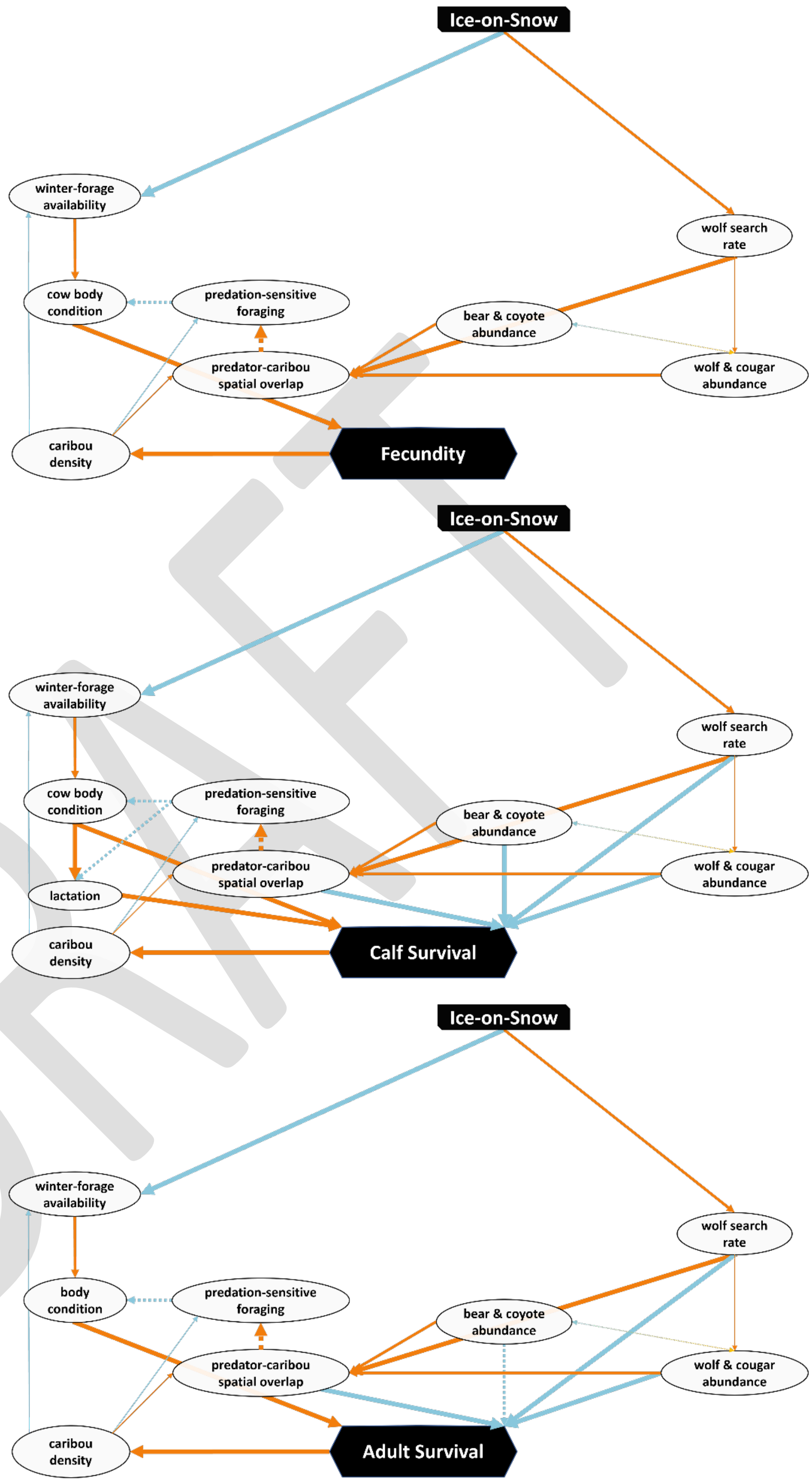
## 6. Ice-on-Snow (Figure 6)

During episodes of unseasonably warm temperature, a thick ice crust can form on top of the snow due to one of two weather events; thawing of the upper layer of snow (typically when solar radiation is strongest) followed by freezing when temperatures drop (typically at night), or rain on snow. Both types of events are expected to occur more frequently as climate change progresses.

**6.1) Predation.** Ice-crusted snow can increase caribou predation by allowing their predators (primarily wolves, but also wolverines and cougars) to move more easily on top of the snow and hence substantially increase their search rate as well as their prey's vulnerability (see also 4.2). Frequent and widespread ice-on-snow events are thus expected to increase predator-caused caribou mortality.

**6.2) Winter forage availability.** Ice-crusted snow can prevent caribou from digging for lichen or early-winter vascular forage, leading to declining body condition and, in extreme scenarios, mass starvation mortalities.

**Figure 6 - DAG representation of the various hypothetical pathways that may lead from an increase in the frequency of ice-on-snow events to increased fecundity, juvenile survival, and adult survival. Orange arrows indicate that an increase at their start-node leads to an increase at their end-node (positive effects). Pale-blue arrows indicate that an increase at their start-node leads to a decrease at their end-node (negative effects). Double-headed arrows represent bidirectional effects, and dashed arrows reflect qualitatively questionable effects. Arrow thickness reflects a qualitative ranking of expected effect size: large (thick), medium, or small (thin).**



## Anthropogenic Disturbance (Figure 7)

Resource extraction activities (timber harvest, oil and gas extraction, and mining), and their associated infrastructure (seismic lines, roads, pipelines, etc.), are thought to be the prime driver of caribou population declines, with mounting evidence that their impacts have so far much exceeded those of natural disturbances (Johnson et al., 2020; Morineau et al., 2023; Stewart et al., 2020). The effects of such anthropogenic disturbances could be synergistic with the effects of climate change (so that the joint impact is smaller or larger than the sum of the individual effects), or simply be of such magnitude that in their presence climate change effects are inconsequential. It is thus crucial to consider the effects of anthropogenic disturbance in conjunction with the effects of climate change.

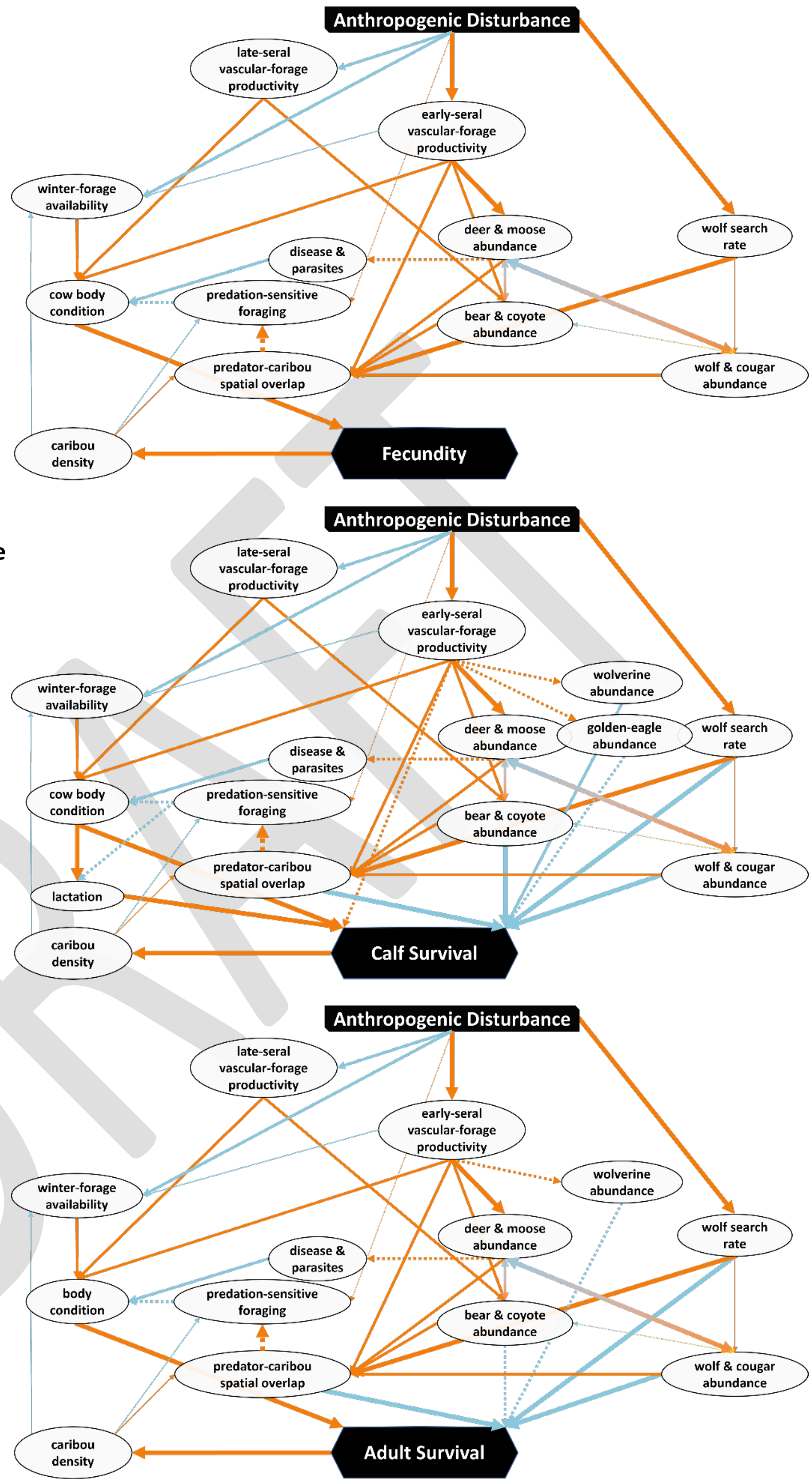
**Timber harvest**, and particularly harvest of old-growth stands, is removing prime lichen habitat, leading to reduced availability of winter forage and hence negative impacts on caribou body condition. Timber harvest also removes late-seral vascular-forage habitat, potentially leading to deteriorated body condition year-round. As noted above (1.1), in the absence of well-planned and executed silviculture treatments, climate change will very likely result in harvested stands regenerating towards new vegetation communities (habitats), dominated by deciduous trees, shrubs, and herbaceous vegetation. Hence, timber harvest is expected to accelerate the long-term process of increasing vascular-plant productivity across caribou ranges, supporting growing and expanding primary-prey populations, and aggravating the impacts of predation on caribou viability (Serrouya et al., 2021). Note that this may also be the case for salvage logging, which has been shown to increase understory productivity and hence primary-prey and predator populations above and beyond the effects of forest die-off alone (Francis et al., 2021; Labadie et al., 2021). Lastly, the current working assumption in caribou conservation is that the negative impacts of old-growth coniferous forest removal are non-linear; there are little impacts up to some disturbance threshold, followed by accelerating impacts beyond that threshold. If this assumption is indeed true, the combined effects of anthropogenic (timber harvest) and natural (pest outbreaks and fire) forest disturbance could have a disproportionally large impact on caribou, pushing many populations over the extirpation edge (Serrouya et al., 2021).

**Other polygonal disturbances**, such as mines and well pads, have a relatively small footprint and are thus not likely to result in significant direct habitat loss, nor benefits to predators or their primary prey. However, caribou may perceive such disturbances as risky, consequently avoiding their 'zone of influence' that may extend well beyond the actual footprints (MacNearney et al., 2021; Polfus et al., 2011; Wilson, 2016). Hence, any active disturbance site may result in substantial 'functional' habitat loss.

**Anthropogenic linear features** (roads, pipelines, powerlines, and seismic lines) may impact caribou in three ways (DeMars & Boutin, 2018; Dickie et al., 2017, 2020; Dickie, Love, et al., 2023; E. J. Newton et al., 2017). First, predators (particularly wolves) travel faster on these features, and preferentially use them, significantly increasing their search rate (i.e., making them more efficient predators). Second, predators can and do use these features to travel deep into 'caribou habitat' (low productivity old-growth forest), thus compromising caribou's main line of defence against predation – spatial separation. Third, caribou tend to avoid these features

((Dickie et al., 2020; Dyer et al., 2001; Fortin et al., 2013; James & Stuart-Smith, 2000; Polfus et al., 2011); but see (Fortin et al., 2008; Mumma et al., 2017; Serrouya et al., 2017; Superbie et al., 2022)), likely because of their enhanced predation risk, resulting in such features causing functional habitat loss and fragmentation (impeding movement). Considering the prevalence of anthropogenic linear features across many caribou ranges, their cumulative impacts are likely substantial.

**Figure 2 - DAG representation of the various hypothetical pathways that may lead from anthropogenic landscape disturbance to increased fecundity, juvenile survival, and adult survival. Orange arrows indicate that an increase at their start-node leads to an increase at their end-node (positive effects). Cyanic arrows indicate that an increase at their start-node leads to a decrease at their end-node (negative effects). Double-headed arrows represent bidirectional effects, and dashed arrows reflect qualitatively questionable effects. Arrow thickness reflects a qualitative ranking of expected effect size: large (thick), medium, or small (thin).**



## Summary and Conclusions

This report provides a comprehensive map of possible pathways by which woodland caribou, both boreal and mountain ecotypes, could be impacted by climate change. The report lists seven instrumental variables, six of which are weather patterns that are expected to shift with climate change:

- **Summer heat**, **length**, and **drought** are presently increasing across caribou ranges due to climate change. These three factors are important drivers of stand-replacing natural disturbance events as well the successional trajectories that follow, and are thus expected to have significant negative effects on caribou viability, operating through both bottom-up (body condition) and top-down (predation) pathways (Figures 1 and 2). Furthermore, these factors are also likely to amplify the existing deleterious effects of anthropogenic landscape disturbance which operate through the same mechanistic pathways (Figure 7).
- **Spring green-up** (the onset of the plant growing season) is shifting earlier with climate change. The effects of this shift on caribou viability are likely negative; it is expected to lead to heightened micropredation, and could result in a phenological mismatch where parturition takes place after the peak in forage quality, compromising lactating cows' access to protein-rich forage when they need it most (Figure 3).
- **Snow depth** is expected to decrease across caribou ranges due to climate change. Whereas shallower snow could benefit some caribou populations by increasing access to winter forage, it is likely to carry an even larger benefit to other (less snow-adapted) large herbivores and consequently increase caribou's exposure to wolf predation, resulting in a net negative effect (Figure 4). For DU9 caribou, who rely on deep snow to reach arboreal lichen, shallower snow may be cumulative to other stressors including predation. The effects of shallower snow are likely to amplify the existing deleterious effects of anthropogenic landscape disturbance which operate through the same mechanistic pathways (Figure 7).
- **Winter severity** is expected to decrease across caribou ranges due to climate change. Milder winters will most likely have a negative effect on caribou population viability, primarily through benefits to primary-prey abundance (and hence predation pressure), but also because of increased thermal stress impacting caribou in winter (Figure 5). Like the effects of longer and hotter summers, and shallower snowpack, the effects of milder winters are likely to amplify the existing deleterious effects of anthropogenic landscape disturbance which operate through the same mechanistic pathways (Figure 7).
- The frequency, severity, and spatial and temporal extent of **ice-on-snow** events are expected to increase across caribou ranges due to climate change. This will undoubtedly carry negative consequences for caribou population viability, limiting access to winter forage and facilitating predator movement (Figure 6).

The relative magnitude of these effects (which are more or less important) is currently unknown. The qualitative ranking used in the DAGs (arrow thickness in Figure 1-7) is based on the authors' subjective evaluation of the current weight of evidence, and should be viewed as such. Moreover, the net effect of a given instrumental variable on a given vital rate is a product of all partial effects along each pathway as well as its synergism with other pathways, a product that may be extremely difficult to quantify.

Recent papers indicate that climate change factors may not be important drivers of caribou population dynamics (Johnson et al., 2020; Morineau et al., 2023; Stewart et al., 2020), or that weather patterns only explain a small fraction of variation in caribou vital rates (DeMars et al., 2021), but is this indeed the case? Would the relative importance of climate change as a driver of caribou population viability increase as its long-term landscape-scale impacts (i.e., radical habitat transformation) manifest? Despite the uncertainty around the relative importance of the pathways listed here, the predominance of negative effects of climate change on caribou ecology that were identified in this review strongly suggests that the answer to this last question is ‘yes’; climate change poses an imminent threat to the long-term persistence of all woodland caribou ecotypes.

## Management and policy recommendations

There is little we can do at this stage to stop the progression of climate change – we cannot affect global emissions at a local scale. This does not mean that we cannot do anything for caribou, just that we need to be strategic around our actions (DeMars et al., 2023; Dickie, Bampfylde, et al., 2023; McLellan et al., 2023). The most climatically vulnerable ranges are those that are expected to experience milder winters and longer hotter summers while also being prone to large-scale stand-replacing events (pest outbreaks, wildfires, or extensive clear-cut logging). We should act now to identify caribou ranges that will be impacted most severely by climate change, as well as ranges that may serve as refugia for decades ahead, by using data, information and tools to monitor real-time climate conditions (https://www.pacificclimate.org/data/bc-station-data ), to identify long-term climate refugia (e.g., https://adaptwest.databasin.org/pages/distribution-and-protection-climatic-refugia/), and post-disturbance habitat recovery (Massey et al., 2023; Stevens-Rumann et al., 2022; White et al., 2022) (https://opendata.nfis.org/mapserver/nfis-change_eng.html). Maintaining caribou on heavily impacted ranges will likely require perpetual intensive predator and/or primary-prey removal, in combination with maternity penning (DeMars et al., 2023).

Disturbance, whether natural or anthropogenic, is bad for caribou. Importantly, post-disturbance forest regeneration under climate change can look very different from historical successional trajectories; hotter and drier conditions mean that fast-growing, drought-tolerant species will likely have the upper hand (Boucher et al., 2020; Brecka et al., 2020; Day et al., 2020; D’Orangeville et al., 2023; Guz et al., 2021; Jorgensen et al., 2023; Molina et al., 2022; Seidl & Turner, 2022; Stevens-Rumann et al., 2022; White et al., 2022; Whitman et al., 2019). Newly harvested or naturally-disturbed stands will be replaced by a different vegetation community than the pre-disturbance community, a community that will, in all likelihood, be inhospitable to caribou. Climate change is thus expected to synergistically amplify anthropogenic disturbance impacts. If the goal is to achieve self-sustaining caribou populations, **new anthropogenic disturbances must be minimized** (including salvage logging; (Francis et al., 2021; Labadie et al., 2021)). To the extent possible, **wildfire suppression and containment should be prioritized** in and around climatically vulnerable caribou ranges. Lastly, efforts should be made to **restore existing**

**disturbance footprints** and **revise silviculture practices** with a view toward progressively hotter and drier conditions.

As evident from examining the causal pathways in our DAGs, the abundance of other large herbivores (moose, elk, mule deer, and white-tailed deer) is a ‘hotspot’ along many of the pathways linking instrumental variables with caribou vital rates. It is in this hotspot that management actions can likely make the biggest difference (DeMars et al., 2023); keeping such primary-prey species at low abundance will be key for maintaining viable caribou populations in a world that will favour the former. This could and should be done in full partnership with Indigenous peoples who rely on these large herbivores for sustenance (Lamb et al., 2023). Many (if not all) caribou ranges will become more biologically productive with climate change. An increased influx of atmospheric heat and solar radiation translates into increased primary production and hence increased production of primary consumer (herbivore) biomass (Serrouya et al., 2021). **Caribou viability may depend on our capacity to funnel this increased biomass production toward human consumers rather than the natural predators they share with caribou**. Note that increased harvest is called for even if the objective is to keep moose and deer abundance stable (rather than reduce it), as a population’s maximal sustainable harvest rate is a product of the population’s carrying capacity and intrinsic growth rate, both of which are expected to increase with climate changes.

To conclude, climate change is expected to push many caribou ranges off the climatic envelope within which caribou populations are self-sustainable. However, we have some control over whether, and if so when these new climatic conditions translate into new ecological conditions that ultimately impact caribou viability. Sustaining and even recovering caribou in the face of climate change is possible, but it will require bold and lasting management actions.

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