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# When is habitat recovered? Understanding the mechanisms of population decline to evaluate habitat recovery for boreal caribou

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## Abstract

Recovering habitat is a central objective for conserving species imperiled by habitat alteration. Yet, determining when habitat is recovered is challenging. For terrestrial wildlife, habitat recovery often focuses on regenerating vegetation, but vegetation changes may provide limited insight as to whether and when habitat is recovered. To be effective as a conservation action, habitat recovery should be linked to demographic responses of the focal species. Moreover, we suggest that habitat recovery be linked to changes in the strength of mechanisms driving population decline. Here, we illustrate such a framework using boreal woodland caribou (*Rangifer tarandus caribou*), which are threatened by altered predator–prey dynamics stemming from habitat alteration. Monitoring habitat recovery is challenging for boreal caribou because demographic effects may take decades to manifest and the spatial scale for demographic monitoring is larger than typical disturbance features or restoration projects. To address these challenges, we propose a continuum of habitat recovery where interim, multi-scale indicators are linked to primary mechanisms underlying caribou population declines. Because habitat recovery varies geographically, indicators may need to be refined on a regional basis. Developing stronger inferences on recovery indicators will require adaptive management, where habitat recovery is implemented over larger spatial extents and longer timeframes.

KEYWORDS

apparent competition, boreal caribou, conservation, endangered species, habitat alteration, habitat restoration, linear disturbances

Our paper should be of broad interest to practitioners, managers, and policy makers involved in habitat protection and recovery for threatened and endangered species.

## 1 | INTRODUCTION

Habitat alteration is a primary cause of species endangerment globally (Caro et al., 2022), prompting conservation strategies to list habitat protection and restoration as central management actions. Protection is generally considered a higher priority, but restoration may be necessary when passive recovery of habitat is insufficient to meet conservation objectives (Possingham et al., 2015). Although these conservation actions seem straightforward, their effectiveness fundamentally depends on understanding what constitutes habitat for a given species, implementing appropriate restoration techniques if necessary to regain such habitat, and determining when habitat is recovered (Miller & Hobbs, 2007). This last point—when is habitat recovered—is particularly challenging given the multi-dimensionality of habitat (Hall et al., 1997). Yet, such a determination can have substantial policy implications for conserving endangered species, especially for those residing in multi-use landscapes where continued habitat alteration by human activities may be permitted if an equal or greater amount of habitat is protected or restored (i.e., habitat offsets for no net loss; zu Ermgassen et al., 2019).

In most instances, protecting and recovering habitat is aimed at stabilizing and recovering threatened populations (Block et al., 2001; Hale et al., 2019). This goal implicitly links habitat to demography, which reflects the definition of habitat by Hall et al. (1997); that is, the resources and conditions allowing populations to be self-sustaining (see Box 1 for habitat-related definitions). Defining habitat recovery therefore requires a understanding of how changes in habitat attributes influence a population's demography. Gaining such understanding, however, is challenging because habitat–demography relationships are scale-dependent, both spatially (i.e., how much habitat is required) and temporally (i.e., how long does it take an altered area to recover). This scale dependency can create circularity when attempting to define habitat recovery. For example, evaluating demographic effects of habitat amount at an appropriate spatial scale often requires making binary determinations of what constitutes habitat at finer spatial scales (i.e., is a given site altered or not?). Also, habitat quality is temporally dynamic, particularly post-disturbance, which can cause temporal variation in the spatial requirements for population persistence (Fahrig, 2001; Johnson, 2007; Van Teeffelen et al., 2012).

One way to address these challenges is to evaluate habitat recovery on a continuum across time and space. Along this continuum, indicators are established to give insights into current habitat conditions and to evaluate whether habitat recovery is tracking toward positive demographic outcomes for the focal species (Watts et al., 2020). To better relate habitat recovery to population recovery, indicators should be indexed to the mechanisms linking habitat alteration to population decline. Because habitat alteration can elicit population decline by a multitude of direct and indirect effects (Fischer & Lindenmayer, 2007), indicators may need to track changes in habitat that extend beyond changes in vegetation.

To illustrate a mechanism-based framework, we consider the case of boreal caribou, an ecotype of woodland caribou currently listed as threatened in Canada (ECCC, 2020). Habitat alteration due to natural and anthropogenic disturbances is a primary cause of population declines of boreal caribou across much of their distribution (ECCC, 2020; Johnson et al., 2020). Consequently, critical habitat for these caribou, as mandated by Canada's federal recovery strategy, requires limiting the cumulative footprint of anthropogenic disturbances (buffered by 500 m) and wildfires <40 years old to <35% of caribou range (the geographic area occupied by a population; Environment Canada, 2011; ECCC, 2020). This threshold correlates to a 60% probability of a population being self-sustaining (Environment Canada, 2011; ECCC, 2020; but see Wilson, 2025).

### BOX 1 DEFINITIONS OF HABITAT-RELATED TERMS

| | |
|---|---|
| Habitat | The resources and conditions conducive to population persistence of the focal species (Hall et al., 1997). |
| Habitat alteration | Modification to a species' habitat that generally decreases habitat quality. |
| Habitat quality | A metric of habitat state as a function of individual performance (e.g., survival and reproduction). Also defined as the per capita contribution of a given area to population growth (Johnson, 2007). |
| Habitat recovery | Process of a disturbed or altered area progressing to a state conducive to population persistence of the focal species. |
| Habitat restoration | Management actions deployed to facilitate habitat recovery. Generally targeted toward legacy disturbances that exhibit delayed or truncated succession. |
| Habitat condition | Habitat state at a given point in time. Incorporates habitat amount and quality. |

Boreal caribou are a prime example of how relating habitat recovery to demographic effects can be challenged by spatial and temporal scales. Demographic monitoring of boreal caribou is typically conducted at the scale of a population's range, which has large spatial extents (e.g., >1000 $km^2$) and was historically characterized by extensive tracts of undisturbed peatlands and mature conifer forest (COSEWIC, 2002; ECCC, 2020; Environment Canada, 2011; Rettie & Messier, 2000). Given these factors, positive demographic effects from habitat recovery may take decades to manifest because of the time required for disturbances to regenerate to suitable conditions, and such regeneration needs to occur over a large spatial scale. In these cases, it is useful to develop interim recovery indicators that encompass multiple temporal and spatial scales. This information will allow managers to gauge whether recovery is tracking toward positive demographic outcomes, without having to wait decades in the absence of tangible information. A continuum of recovery indicators can also guide habitat restoration by identifying disturbances with truncated recovery (e.g., legacy seismic lines; van Rensen et al., 2015), prioritizing disturbances based on their relative influence on population decline, and evaluating the efficacy of restoration actions.

Boreal caribou are also an example of why monitoring habitat recovery should extend beyond tracking changes in vegetation. Habitat alteration impacts caribou through multiple mechanisms that ultimately result in unsustainable rates of predation (Frenette et al., 2020; Fryxell et al., 2020; Serrouya et al., 2021). In instances where predators have been reduced by management, caribou populations have stabilized and increased without concurrent changes in vegetation (Lamb et al., 2024; Serrouya et al., 2019). Although caribou typically require large tracts of undisturbed forest to be self-sustaining (but see Neufeld et al., 2021 for an outlying example), the critical aspect of these conditions is that they support low densities of predators and provide refugia to caribou. Because of this relationship, indicators of habitat recovery should reflect how vegetation changes lead to changes in the large mammal community that ultimately decrease predation pressure on caribou.

Understanding when habitat is recovered has substantial policy implications for caribou conservation. Many caribou ranges overlap areas containing high-value natural resources (Fortin et al., 2020; Hebblewhite, 2017). Development of these resources has continued and accelerated in most ranges (Maltman et al., 2024; Nagy-Reis et al., 2021), despite boreal caribou being designated as threatened for over two decades (COSEWIC, 2002; ECCC, 2020). Policies allowing ongoing development suggest that socioeconomic factors will continue to influence how caribou are managed (DiSilvestro & Irvine-Broque, 2023; Fortin et al., 2020; Government of Alberta, 2020, 2024; Hebblewhite, 2017). Halting population declines and sustaining caribou in these multi-use landscapes will require protecting remaining intact areas, taking actions to recover habitat, and understanding when previously altered areas are recovered (ECCC, 2020; Ray, 2014).

For boreal caribou, a key element of habitat recovery is reducing the cumulative area of disturbance within caribou range (ECCC, 2020). This metric fundamentally depends on defining whether an area is considered disturbed or not. Current federal criteria for determining disturbed versus undisturbed vary by disturbance type. Areas burned by forest fire are considered disturbed if the fire occurred within the last 40 years (Environment Canada, 2011), a delineation informed by caribou preference for mature forests (Dalerum et al., 2007; Schaefer & Pruitt Jr., 1991). For anthropogenic disturbances, an area is considered disturbed if it remains visible on Landsat imagery at a scale of 1:50,000 (Environment Canada, 2011; ECCC, 2020, 2024). This criterion was necessarily simple, given the information and technology available at the time, the magnitude of disturbance, and the spatial extent of caribou ranges. This criterion also provides a repeatable method for defining disturbance and setting management targets, but it has several limitations for evaluating habitat recovery and condition. First, it assumes that restoring vegetation to its pre-disturbance visual state means that the disturbance-mediated mechanisms of population decline are no longer operating, an assumption that does not always hold and remains untested for caribou (McNeil et al., 2020; Palmer et al., 1997; Schrott et al., 2005). Moreover, using vegetation regeneration as a proxy for habitat recovery may become increasingly unreliable under climate change where the northward expansion of apparent competitors and predators may create conditions unconducive to caribou persistence despite vegetation recovering to its pre-disturbance state (Bastille-Rousseau et al., 2018; Dickie et al., 2024; Kennedy-Slaney et al., 2018). A second drawback to the visual criterion for anthropogenic disturbances—or any binary approach—is that it provides limited insight into current habitat condition. For example, two ranges could have similar disturbance proportions, yet habitat conditions—and demographic impacts—could vary substantially between the two because of differences in disturbance types, disturbance ages, biogeoclimatic conditions, and rates of succession. A third drawback is that the visual criterion provides limited ability to predict when habitat might be recovered (i.e., how long does it take for a feature to no longer be visible?). Recovery Indicators indexed to disturbance-mediated mechanisms of decline have the potential to better predict when negative demographic impacts are expected to diminish (discussed further below), which can better inform planning of short- and long-term management strategies.

Here, we propose complementary indicators of habitat recovery that directly relate to two primary mechanisms associated with caribou population declines: disturbance-mediated apparent competition (DMAC) (Frenette et al., 2020; Fryxell et al., 2020; Serrouya et al., 2021) and altered predator behavior stemming from linear disturbances (LDs) (e.g., roads, pipelines and seismic lines). We assess how the strength of each mechanism may change as vegetation recovers and how such changes can serve as indicators of habitat recovery at two spatial scales: the site scale (i.e., an individual disturbance feature) and the range scale. We augment these vegetation-based indicators with indicators tracking changes in the large mammal community. Note that with our focus on recovery indicators, we do not provide recommendations on how to recover or restore habitat per se, as such information can be found elsewhere (e.g., Bentham & Coupal, 2015; Filicetti et al., 2019; Government of Alberta, 2018; Kleinke et al., 2022; Lacerte et al., 2021).

## 2 | INDICATORS OF HABITAT RECOVERY INFORMED BY APPARENT COMPETITION

DMAC is a bottom-up process that ultimately results in unsustainable rates of predation for caribou (Frenette et al., 2020; Fryxell et al., 2020; Serrouya et al., 2021). The process is initiated when disturbances convert mature forest to early seral conditions, which increases forage for other ungulates, such as moose (*Alces alces*) and deer (*Odocoileus* spp.; hereafter, apparent competitors). As populations of apparent competitors increase from these forage subsidies, predator populations (e.g., wolves [*Canis lupus*]) also increase, leading to increased predation pressure on caribou and population declines (DeCesare et al., 2010; Seip, 1992; Serrouya et al., 2021).

The strength of DMAC is influenced by the timing, quality, and quantity of forage production for apparent competitors post-disturbance (Gagné et al., 2016; Neufeld et al., 2021; Superbie et al., 2022). As forage production declines, populations of apparent competitors and predators should subsequently decline, leading to decreased predation pressure on caribou. Given this expectation, an intuitive indicator of habitat recovery for caribou is when forage production for apparent competitors returns to pre-disturbance levels. Although tracking forage dynamics can be done by field sampling (e.g., Crête & Jordan, 1982), recent approaches have used remotely sensed indices of vegetation dynamics (Esmaeili et al., 2021; Pettorelli et al., 2005; Serrouya et al., 2021). Approaches using remotely sensed data are particularly advantageous for caribou given the large spatial scales and high number of disturbance sites within caribou range.

We used remotely-sensed data to develop DMAC-informed indicators of habitat recovery at the site scale (Box 2). Specifically, we used Enhanced Vegetation Index (EVI) data to track changes in ΔEVI, which is the difference between the peak and minimum EVI values within a given year. The ΔEVI metric is highly influenced by phenological changes in deciduous vegetation and therefore indexes forage quantity and/or quality for deciduous browsers such as moose and deer (Baribeau et al., 2022; Crête & Bédard, 1975; Thomas, 1990). This metric has been positively correlated with moose density (Dickie et al., 2022; Serrouya et al., 2021), deer density (Dickie et al., 2024) and moose occupancy (Gagné et al., 2016). Our analyses suggest that, on average, ΔEVI returns to pre-disturbance values approximately 40 years post-harvest and approximately 60 years post-burn (Box 2 and Figure B2.1). Abandoned well pads did not return to pre-disturbance values within the timespan of our analyses. Note that these estimated timelines for recovery do not account for the amplitude of change in ΔEVI among the disturbance types, which can influence the strength of DMAC prior to recovery (Box 2 and Figure B2.1). Also, while we report mean values, results could be summarized by ecosite if ΔEVI recovery varies by biogeoclimatic conditions or obtained for each individual site to assess recovery on a site-by-site basis.

Site-scale indicators based on ΔEVI can be extended to the range-scale by calculating the proportion of the range that is below the ΔEVI-informed recovery threshold, similar to how disturbance is tracked in the federal recovery strategy (Environment Canada, 2011; ECCC, 2020). For a given range, the proportions of unrecovered cutblocks, fires, and other disturbance features can be individually tracked or summed to give an overall proportion of disturbed habitat. Importantly, by explicitly linking habitat recovery to time (Box 2), predictions can be made as to when habitat is expected to be recovered. Such information can then inform management planning, particularly when deploying actions to address DMAC that are considered short-term but often lack a predicted timeframe for their need (e.g., Lamb et al., 2024).

Range-scale indicators based on vegetation changes should be augmented by indicators indexing densities of apparent competitors and predators that are conducive to stable caribou populations. Such indicators are necessary to ensure vegetation changes are leading to caribou habitat recovery. Population stability for caribou has been commonly linked to wolf density (Bergerud, 1988; Bergerud & Elliot, 1986; Serrouya et al., 2021). For boreal caribou, recent studies suggest stable populations require wolf densities ≤3/1000 km$^2$ (Fryxell et al., 2020; Neufeld et al., 2021) or even as low as 1.8/1000 km$^2$ (Serrouya

## BOX 2 TRACKING FORAGE DYNAMICS POST-DISTURBANCE

To track forage dynamics pre- and post-disturbance, we used Landsat data (30-m resolution; temporal range: 1984–2023) to model temporal changes in the annual amplitude of the EVI (ΔEVI; see the Supporting Information for further details and data used). ΔEVI is sensitive to changes in deciduous vegetation and thus indexes forage production for moose and deer. For this example, we randomly sampled cutblocks ($n = 100$), fire polygons ($n = 100$), and abandoned well pads ($n = 100$), all with known dates-of-creation, within boreal caribou ranges in northeastern British Columbia and Alberta. For each disturbance type, we fit a generalized additive mixed model to the ΔEVI data, specifying years since disturbance as the smoothing term and individual site as a random effect. As an indicator of habitat recovery for caribou, we calculated the geometric mean of ΔEVI pre-disturbance to serve as a baseline as to when vegetation had returned to pre-disturbance levels.

Cutblocks showed the highest increase in ΔEVI post-disturbance and, on average, returned to pre-disturbance values after approximately 40 years (Figure B2.1). Fires had a more muted response in ΔEVI compared to cutblocks and, on average, returned to pre-disturbance values approximately 60 years post-fire. Well pads had a slightly higher increase in ΔEVI compared to fires and, on average, did not return to pre-disturbance values for at least 30 years. The temporal range of the well pad data limited post-disturbance monitoring beyond 30 years so estimating recovery for this disturbance type is not yet possible. However, well pads are known to have truncated regeneration due to the removal of native soil, soil compaction, and altered hydrology (Lupardus et al. 2019).

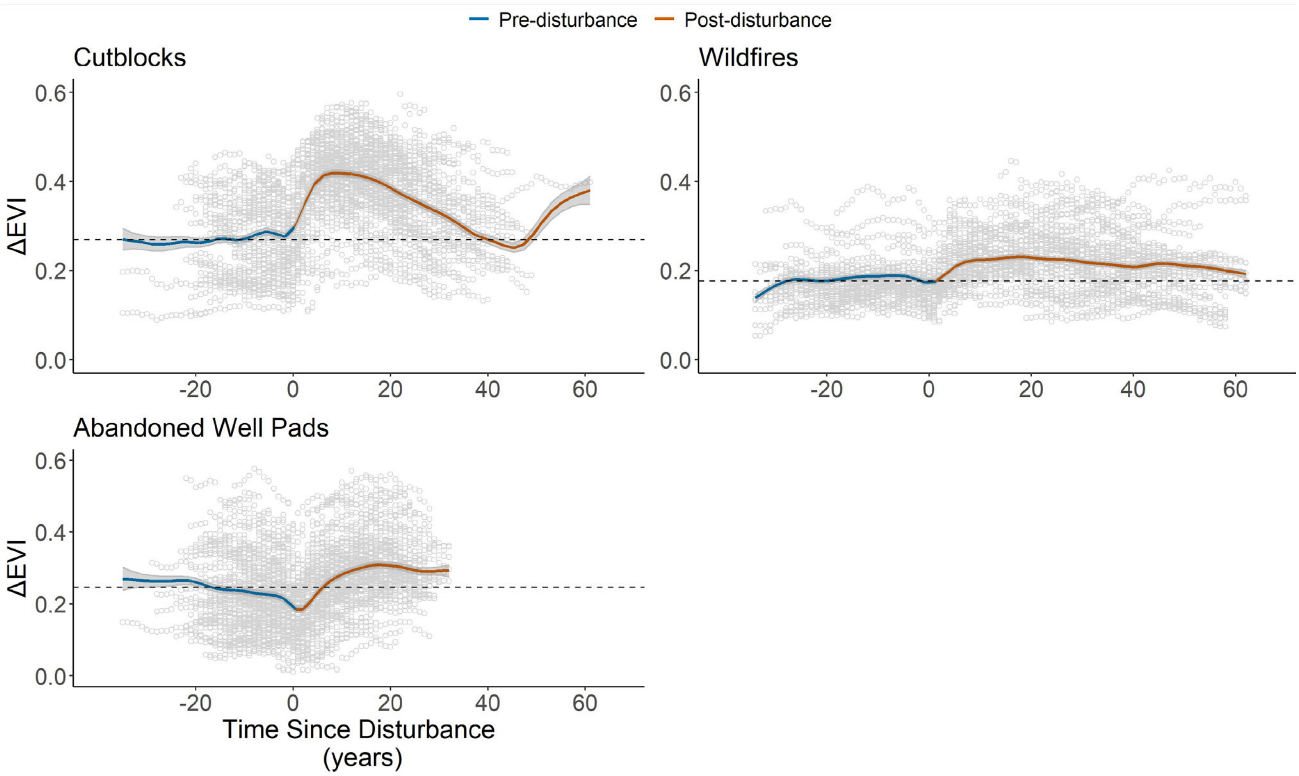


FIGURE B2.1 Temporal changes in ΔEVI pre- and post-disturbance in cutblocks, wildfires, and well pads (site-years indicated by gray points). An indicator of habitat recovery for caribou is when ΔEVI returns to pre-disturbance levels (horizontal dashed line = geometric mean of ΔEVI pre-disturbance).

et al., 2021). Indicators based on densities of apparent competitors should largely reflect the target wolf density (Messier, 1994; Serrouya et al., 2017). For ranges where moose are the sole apparent competitor, empirical and theoretical estimates suggest moose density needs to be $<0.10/\text{km}^2$ to achieve a wolf density of $\leq 3/1000\ \text{km}^2$

(Fuller, 1989; Kittle et al., 2015; Messier, 1994; Neufeld et al., 2021). Serrouya et al. (2021) also reported that stable caribou populations were associated with moose densities of <0.03/km$^2$, but their study included ranges containing other apparent competitors such as white-tailed deer. Note that in systems where white-tailed deer are established and abundant, wolf densities often exceed 20/1000 km$^2$ (Fuller et al., 2003), highlighting that robust white-tailed deer populations and caribou populations are unlikely to coexist.

For some caribou ranges, predation by black bears can be a significant driver of population decline (Mahoney & Virgl, 2003; Pinard et al., 2012; Rettie & Messier, 1998). Black bears, however, do not fit neatly within the DMAC hypothesis. As omnivores, bears are not solely dependent on ungulates as prey, and disturbances may directly increase bear populations by providing subsidies in vegetative forage (Brodeur et al., 2008; Schwartz & Franzmann, 1991). As such, estimating a DMAC-informed indicator of habitat recovery based on bear density is difficult. Understanding the influence of disturbances on the population dynamics between black bears and caribou remains a key knowledge gap in caribou conservation.

## 3 | INDICATORS OF HABITAT RECOVERY INFORMED BY LINEAR DISTURBANCE MECHANISMS

LDs can negatively impact caribou through multiple mechanisms, but those having the highest impact stem from how LDs alter the movement behavior of predators, particularly canids (DeMars et al., 2023; DeMars & Boutin, 2018; Dickie et al., 2020; Dickie, Love, et al., 2023). Three primary mechanisms are associated with altered predator behavior. First, LDs enhance predator movement efficiency, increasing their encounter rate with prey, including caribou (Dickie, Serrouya, McNay, & Boutin, 2017; Gable et al., 2023). Second, by increasing foraging efficiency, LDs shrink the territory size of wolf packs, leading to increased wolf density at a landscape scale (Dickie et al., 2022). Third, LDs facilitate predator movement into caribou refugia, increasing rates of caribou–predator encounter (DeMars & Boutin, 2018; Mumma et al., 2018).

For LDs, site-scale indicators of habitat recovery should index predator use and movement speed. Ideally, indicators should reflect when predator use (or selection) and movement speed on an LD are equal to values observed in mature forest. Separate indicators, however, may not be necessary as use and movement speed are generally correlated (Dickie, Serrouya, DeMars, et al., 2017; Finnegan et al., 2018; Tattersall et al., 2023). Two potential indicators can be identified based on studies evaluating how regenerating vegetation impacts the movement speed of wolves (e.g., Dickie, Serrouya, DeMars, et al., 2017; Finnegan et al., 2018; Figure 1). The first indicator is when vegetation regenerates to an average height of 0.5 m, which equates to a sharp decline in wolf movement speed on LDs (Dickie, Serrouya, DeMars, et al., 2017; Finnegan et al., 2018). Although the demographic effects on caribou from this slowdown in predator movement are unknown, this indicator reflects when the magnitude of movement-based mechanisms is expected to diminish. The second indicator is when average vegetation height exceeds 4.0 m, which indexes when wolf movement speed on LDs approximates their speed in mature forest (Dickie, Serrouya, DeMars, et al., 2017). Both of these LD indicators can be evaluated by field sampling, but approaches using airborne- or satellite-derived data of vegetation structure (e.g., Dickie, Hricko, et al., 2023; Killion et al., 2023) may be more practical given the extensive distribution of LDs in many caribou ranges (Johnson et al., 2019; Nagy-Reis et al., 2021).

LDs have been the focus of alternative restoration actions aimed at limiting predator movement. These approaches, known as functional or process-based restoration (Ford, 2021; Keim et al., 2021), aim to restore biological processes to their pre-disturbance state and may not necessarily result in an area being restored to its previous structural state (c.f. ecological restoration). Examples of functional restoration treatments include tree-felling and intensive deployment of coarse woody debris. Although functional restoration is expected to have more immediate effects on predator use and movement speed, this approach has a number of uncertainties, including how long treatment effects last, whether treatments can be easily refurbished if effects wane, and whether these treatments result in functional habitat for caribou. Because our focus here is on identifying indicators of habitat recovery associated with self-sustaining caribou populations, we do not consider indicators for functional restoration.

Range-scale indicators of recovery should ideally index how LD density impacts predator foraging efficiency and abundance and, ultimately, caribou demography (Figure 1). As LDs recover over larger spatial scales, declines in the movement speed of predators should translate to declines in kill rates. For wolves, declines in kill rates may result in larger territory sizes, leading to decreased wolf densities (Dickie et al., 2022). Currently, estimates for most of these relationships are lacking, with only one observational study showing an association between low densities of LDs (0.11 km/km$^2$) and low densities of wolves (3.1 /1000km$^2$; Neufeld et al., 2021). Several other studies, however, have estimated effects of LD density on caribou demography. To date, these

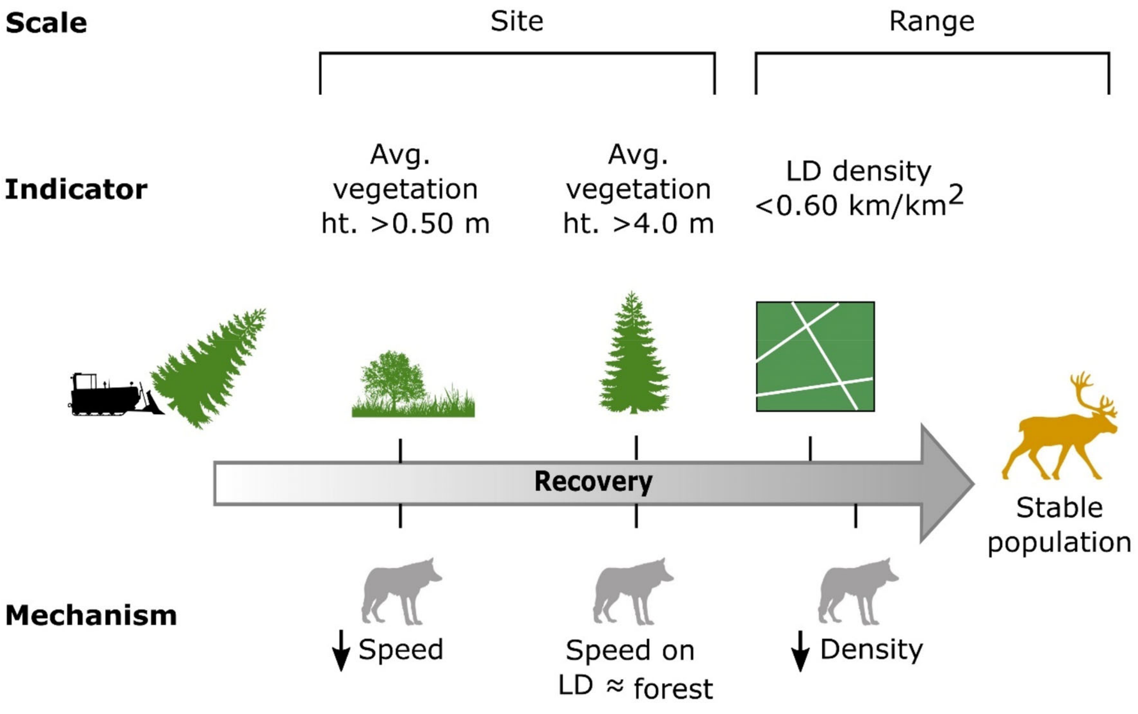


FIGURE 1 The continuum of caribou habitat recovery after a linear disturbance. Recovery indicators are proposed that relate vegetation recovery to changes in predator movement and density. Habitat is considered recovered when caribou populations are stable without active management (i.e., self-sustaining).

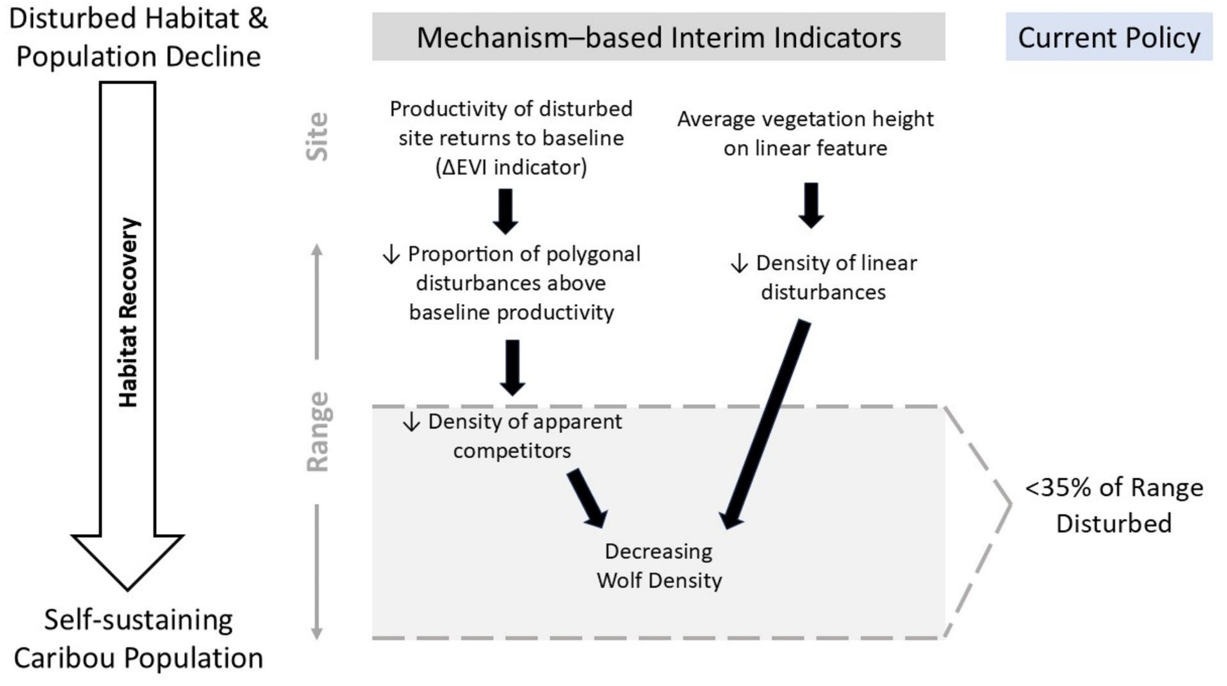


FIGURE 2 Conceptual framework illustrating how mechanism-based interim indicators can complement current policy mandated by Canada's federal recovery strategy for boreal caribou. Under the federal strategy, caribou populations are considered to have a 60% probability of being self-sustaining when their ranges have ≤35% disturbed area (as defined by federal criteria for disturbance). This threshold is assumed to reflect the biotic conditions required for caribou persistence; however, it remains uncertain whether these conditions return as vegetation recovers in highly disturbed ranges. Mechanism-based interim indicators provide a more direct measure of these biotic conditions (e.g., productivity and densities of apparent competitors and predators—see Table 1 for proposed values), offering additional insights into whether habitat recovery is progressing toward the ultimate goal of self-sustaining caribou populations. Gray shading bounded by dashed lines highlights uncertainty in the timing of recovery of apparent competitor and predator densities that are compatible with caribou persistence.

**TABLE 1** Summary of potential indicators of habitat recovery for boreal caribou at two spatial scales.

| Mechanism | Scale | Indicator | Rationale |
|---|---|---|---|
| Disturbance-mediated apparent competition (DMAC) | Site | Forage biomass for apparent competitors (e.g., moose and deer) is equal to pre-disturbance values. Forage biomass can be indexed by ΔEVI (Box 2). | As a bottom-up process, the strength of DMAC is influenced by the amount of forage available to apparent competitors post-disturbance. |
| | Range | Proportional area of polygonal disturbances within caribou range above baseline productivity. Recovery from disturbance estimated by disturbance type or can be estimated on a site-by-site basis using ground-based or remotely sensed indicators (Box 2). The current federal recovery strategy mandates that disturbances should be <35% of caribou range. | As productivity declines, abundance of apparent competitors should decline. |
| | Range | Moose density <0.10/km$^2$ | Confirm habitat conditions within caribou range support low densities of apparent competitors. |
| | Range | Wolf density <3.0/1000 km$^2$ | Confirm habitat conditions within caribou range support low densities of predators. |
| Altered predator behavior from linear disturbances (LDs) | Site | Avg. vegetation ht. on LD >0.5 m | Predator movement speed declines sharply after this initial indicator is reached. |
| | Site | Avg. vegetation ht. on LD >4.0 m | Predator movement speed on LDs approximates speed in mature forest. |
| | Range | LD density <0.60 km/km$^2$ | Estimated threshold of LD density below which caribou populations are stable. |
| | Range | Wolf density <3.0/1000 km$^2$ | Confirm habitat conditions within caribou range support low densities of predators. |

*Note*: Indicators are indexed to putative mechanisms underlying population declines of boreal caribou. Numeric values for indicators should be viewed as potential starting values that can be refined based on future studies and adaptive management. Habitat at the scale of a caribou range is recovered when caribou populations are stable.

estimates have been derived from simulation-based studies using theoretical predator–prey models (Dickie, Love, et al., 2023; McCutchen, 2007; Serrouya et al., 2020; Spangenberg et al., 2019). Although studies vary in the estimated threshold of LD density that correlates with caribou population stability, all suggest that the threshold needs to be low (e.g., <1 km/km$^2$, potentially <0.6 km/km$^2$, see Dickie, Love, et al., 2023 for a review). Empirical validation of these theoretically derived thresholds is needed, although disentangling LD effects from apparent competition is challenging because, in many caribou ranges, LDs co-occur with polygonal disturbances. Nevertheless, thresholds could be tested using an adaptive management approach where LDs are restored over progressively larger spatial scales.

## 4 | DISCUSSION

In his seminal paper describing the declining population paradigm, Caughley (1994) advised that management actions be directed at the causal agents of decline. For species threatened by habitat alteration, habitat recovery is a primary focus, yet understanding its effectiveness can be challenging, particularly for species requiring habitat conditions that may take decades to recover. To address this challenge, we extended Caughley's (1994) logic by proposing that habitat recovery be viewed on a continuum with interim indicators indexed to the primary mechanisms of decline. This extension aligns with increasing calls to use ecological theory to guide habitat restoration (DeMars et al., 2023; Lake et al., 2007; Silliman et al., 2024; Török & Helm, 2017) and here we put an emphasis on how theory can also inform evaluating habitat recovery after management actions have been implemented.

For caribou, we proposed specific indicators based on apparent competition and altered predator movement on linear features, but other mechanism-based criteria could be used. For example, criteria could be based on moose selection for disturbances, potentially varying by biogeoclimatic conditions, which could yield thresholds with different timespans for recovery than ours (e.g., 36 years, Hessami et al., 2025; 25 years, Mumma et al., 2021). Moreover, moose selection could be related to ΔEVI to better inform when apparent competition is expected

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to diminish, which could differ from the timeline associated with our criterion (i.e., when ΔEVI returning to its pre-disturbance baseline). Different criteria may also vary in their effectiveness in tracking a given mechanism, particularly if the criterion does not directly measure the metric of interest. Vegetation height on an LD, as an example, does not directly measure predator movement speed, whereas estimates of predator density directly measure a key component of apparent competition. To that end, proposed criteria should undergo further investigation to determine how closely they track a given mechanism and subsequently caribou demography, which is the ultimate assessment of when caribou habitat is recovered.

A key limitation to our proposed framework is that, unlike the 35% disturbance threshold mandated by the federal recovery strategy for boreal caribou (ECCC, 2020; Environment Canada, 2011), most of our indicators have not been explicitly related to a probability for self-sustaining caribou populations. Such analyses should be done as data become available (sensu Serrouya et al., 2021). Despite lacking these assessments, all of our indicators have theoretical and/or empirical foundations and directly measure the biotic conditions thought to influence caribou population persistence (i.e., vegetation productivity and densities of apparent competitors and predators). Collectively, our proposed indicators can complement the federal recovery strategy (Figure 2) by providing multiple lines of evidence, an approach known to help increase certainty for managers when making conservation decisions (Cook et al., 2012; Gillson et al., 2019). Using multiple indicators will also help address some of the uncertainty associated with the federal 35% threshold. At this threshold, caribou populations have a 60% probability of being self-sustaining, and the 35% value was based on an initial regression analysis, where 70% of the variation in juvenile recruitment was explained by disturbance in caribou range (Environment Canada, 2011). Recent analyses, however, suggest that the uncertainty around this threshold may be higher (disturbance explained 53% of the variation in juvenile recruitment and only 14% in adult female survival, Johnson et al., 2020; disturbance had low causal attribution (17.6%) to recruitment, Wilson, 2025). Such uncertainty is likely to increase in the coming decades due to accelerating effects from climate change (DeMars et al., 2023), further necessitating the monitoring of other aspects of caribou habitat beyond landscape disturbance.

Our proposed framework has other limitations. First, we constrained the scope to apparent competition and altered predator movement on linear features, but caribou populations may be impacted by other mechanisms (DeMars et al., 2023). Thus, our interim recovery measures should not be considered an exhaustive list. Second, the utility of our mechanism-based indicators assumes that these mechanisms will also have a high influence on habitat recovery going forward. Given the uncertainty associated with climate change, continued monitoring of caribou populations will be necessary to ensure that recovery indicators are effectively tracking the mechanisms with the strongest influence on habitat recovery.

By developing interim indicators of habitat recovery that complement the existing federal recovery strategy, our proposed framework provides additional insights into current habitat conditions and projected timelines for recovery. Such information is necessary to formulate conservation strategies that often must account for ongoing human activities and natural disturbances within caribou range (e.g., Government of Alberta, 2020), and can inform analyses of habitat gain versus loss to understand the key metric of net rate of change (Nagy-Reis et al., 2021). Quantitative, empirical indicators such as ours also provide tangible goals for managers to work toward, thus incentivizing experimentation with novel techniques and practices to achieve management targets sooner. These targets may differ, at least in the short term, from the 35% disturbance threshold of the federal recovery strategy (ECCC, 2020; Environment Canada, 2011), but we do not see these potential differences as problematic because our indicators are meant to provide inferences as to whether habitat recovery is trending toward positive demographic outcomes for caribou (i.e., no single interim indicator in and of itself is indicative of habitat recovery). Moreover, our framework arrives at the same endpoint as the federal recovery strategy; that is, habitat is recovered when caribou populations are self-sustaining.

Uncertainty between our proposed indicators and caribou demography should not preclude implementing a framework that considers habitat recovery on a continuum with multiple interim indicators. Although the exact demographic effects on caribou of a particular indicator may not be known, useful generalizations can still be made. For example, if the density of apparent competitors is decreasing as vegetation recovers, then the effect on caribou demography is likely to be positive. In contrast, if the density of apparent competitors remains unchanged or is increasing, then vegetation recovery alone is unlikely to lead to habitat recovery for caribou, and confounding factors such as climate change need to be considered (DeMars et al., 2023; Dickie et al., 2024). To that end, information from interim indicators can play an important role in adaptive management, an approach that will likely be necessary to successfully stabilize and recover many caribou populations (ECCC, 2020; Serrouya et al., 2019).

We proposed values for many of our indicators based on a literature review of studies conducted over the broad distribution of boreal caribou. As such, these estimated values may be subject to geographic variation. For example, we illustrated that ΔEVI within cutblocks of northeast British Columbia and Alberta recovered to pre-disturbance values by 40 years, on average, but this time-frame could vary based on biogeoclimatic conditions that influence rates of succession. Our estimate of moose density for stable caribou populations could also vary geographically depending on the contribution of other prey to wolf diet in different systems (Latham et al., 2013; Sovie et al., 2023). Ultimately, our indicators may be modified or improved by further empirical testing. We suggest that the best approach for obtaining robust indicators is through an adaptive management framework where a caribou range (or sample of ranges) is progressively restored and monitored through space and time. For caribou populations that are small and rapidly declining, intervention-forward adaptive management may be necessary where population management is deployed to maintain caribou on the landscape then gradually removed as caribou habitat progresses on the continuum to recovery (Dickie, Ford, et al., 2023). Currently, large-scale restoration has been initiated within a few caribou ranges in western Canada, but the spatial and temporal scales are not yet sufficient to evaluate demographic responses of caribou, apparent competitors, and their predators (Dickie, Sherman, et al., 2023; RICC, 2020; Tattersall et al., 2020). To better inform efforts to recover habitat now and in the future, continued testing of restoration effects at larger spatial scales is urgently needed.

We focused on proposing indicators that were logistically feasible to monitor on a consistent basis. That said, some indicators will be more difficult and costly to monitor than others, particularly those indexing changes in the large mammal community. These indicators, though, are critical to assessing habitat recovery for caribou given that this species can survive in a wide range of vegetation conditions (e.g., boreal forest, Arctic tundra, interior rainforest) provided predator densities are low (Bergerud, 1996). Although monitoring costs may appear high for some indicators, such costs may constitute only a small fraction of the multi-million-dollar costs associated with habitat restoration for a typical caribou range (Johnson et al., 2019; Nagy-Reis et al., 2020). Given these high restoration costs, having multi-scale interim indicators of recovery is imperative for evaluating the effectiveness and cost-efficiency of restoration actions.

Protecting and recovering habitat have long been recognized as necessary management actions for maintaining boreal caribou in their current distribution (ECCC, 2020; Environment Canada, 2008; Ray, 2014). Yet, actions to recover habitat have only been implemented in a small proportion of caribou range (DeMars et al., 2023) and many ranges continue to undergo habitat alteration (Maltman et al., 2024; Nagy-Reis et al., 2021). While financial constraints limit the amount of habitat restoration, we suggest that uncertainty in the effectiveness of restoration (e.g., Tattersall et al., 2020) and the lack of a clear definition of habitat recovery are also factors. To that end, our framework of mechanism-based indicators that evaluates habitat recovery on a continuum may help incentivize the deployment of habitat restoration and protection over the spatial scales necessary to meaningfully impact caribou demography and conservation.

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## DATA AVAILABILITY STATEMENT

Data and R code used in our analyses are available within the Zenodo repository (DOI: 10.5281/zenodo.13367837; note: these data are not yet published but can be accessed via the following link: https://zenodo.org/records/13367837?preview=1&token=eyJhbGciOiJIUzUxMiJ9.eyJpZCI6ImQ1NWIwYmQyLWNlNjQtNGIwNC1hZjM4LTg5NjdhZDNkODIzYiIsImRhdGEiOnt9LCJyYW5kb20iOiI4NTc5ZDI5ZjNkYTZjZTI1ZDQ4MGQ3YzJlYjRjMTU2YiJ9.Y5JJ1oT9JD1fGfKXKoc5SbmakV8a6xjpl5-orxfyg6YuxXWlQy_xQkjauKShpnniankTKzbAAINTqzkIOPwkKg). Additional information on data sources can also be found in the Supporting Material.

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## SUPPORTING INFORMATION

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

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