Developing functional restoration guidance for forestry roads in Ontario from a boreal caribou perspective

Summary

Under the bilateral conservation agreement, Ontario and Canada share a goal of sustaining healthy local populations of threatened boreal caribou. Achieving this goal requires effective management of human-caused habitat disturbance associated with natural resource development and its supporting infrastructure. Roads and other linear features can increase caribou risk by facilitating movement of predators and their primary prey, while also creating early-seral forage and other conditions that alter predator-prey relationships. However, clear and defensible criteria for determining when forestry roads are functionally restored remain limited in Ontario.

Using data from a large-scale, multi-year camera-trap study in northwestern Ontario, we examined use of forestry roads across a gradient of regeneration, access, and road condition by five mammals that directly and indirectly affect caribou: wolf, black bear, moose, Canada lynx, and snowshoe hare. We identified factors associated with road-use intensity and compared use on non-primary roads with use at forest reference sites. The study focused primarily on roads left to regenerate naturally, while also including a limited number of sites with decommissioning measures such as berms, scarification, water-crossing removal, and planting or seeding.

All five focal mammals used non-primary roads more than forest reference sites during at least part of the year. This community-wide response indicates that assessment focused on a single species is unlikely to capture the full set of road functions relevant to caribou. Road–forest differences were strongest and most consistent during the snow-off season, which overlaps with calving and post-calving, although the study did not directly measure calf mortality or recruitment. Ease of movement was the most consistently supported driver of road use, while vegetation structure, visibility, forage and cover conditions,

human disturbance, and landscape context shaped responses differently among species and seasons. Wolves and lynx used sampled roads less near primary roads, showing that low use of an individual road can reflect avoidance of broader human disturbance rather than diminishing road function. No single vegetation measure, including vegetation height, adequately represented functional recovery across the focal mammal community.

Motorized access was associated with greater road use by wolves in both seasons and by lynx during snow-on. Roads with traffic also tended to retain shorter vegetation, lower hiding and shrub cover, greater graminoid cover, and faster walking conditions. Decommissioning measures reduced traffic at some sites but did not consistently eliminate access, as vehicles could circumvent barriers, enter through connecting roads, or continue using roads with all-terrain vehicles and snowmobiles.

Our findings support a proposed framework for assessing functional restoration based on four linked components: 1) effective control of year-round motorized access; 2) reduction of movement, visibility, and vegetation-mediated advantages; 3) use by a focal mammal community approaching appropriate forest reference conditions; and 4) interpretation within the relevant ecological, seasonal, and landscape context. The framework identifies candidate indicators and directions of change, but validated reference ranges, thresholds, and decision rules remain to be developed. The study also does not directly measure effects on caribou survival, recruitment, or population persistence. Avoiding new road access in important caribou habitat therefore provides greater certainty than relying on future restoration to reverse ecological effects.

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Introduction

Boreal caribou (*Rangifer tarandus caribou*, herein caribou) are threatened in Ontario and across Canada. Their primary threat is human-caused habitat disturbance, as they rely on large undisturbed areas of mature conifer forest often intermixed with peatlands for winter forage and refuge from predators and their primary prey (ECCC 2020). Through the 2022 bilateral conservation agreement between Canada and Ontario, the two governments have articulated a shared intent to support caribou conservation and the goal of sustaining healthy local populations across boreal ranges. Among other things, the agreement acknowledges that achieving self-sustaining local populations will require a combination of protective and management measures, along with habitat restoration, with particular emphasis on managing cumulative disturbance within caribou ranges. Caribou conservation measures are also recognized for their broader benefits, including supporting biodiversity, as well as contributing to climate change mitigation and adaptation through sustainable natural resource management (ECCC & MECP 2022).

Managing natural resource development and associated infrastructure effectively, including roads and other linear features, is critical to achieving self-sustaining caribou populations. Resource development activities convert mature forest to younger seral stages that attracts caribou predators through their primary prey, increasing caribou predation risk via apparent competition (Serrouya et al. 2021, Wittmer et al. 2005).

Linear features further facilitate movement of predators and their primary prey on the landscape (Dickie et al. 2020, 2017a, DeMars and Boutin 2017, McKenzie et al. 2012) and directly increase overlap between caribou and their predators independent of apparent competition (Mumma et al. 2018). Caribou are known to avoid roads and other linear features (Mumma et al. 2019, 2017, DeMars and Boutin 2017), with avoidance also being positively related to human disturbance levels such as road width, traffic density, and human activity (Leblond et al. 2013, Polfus et al. 2011).

Much research indicates that cumulative disturbance and associated predator-prey dynamics remain the primary drivers of caribou population decline (ECCC 2020, Frenette et al. 2020, Fryxell et al. 2020, Serrouya et al. 2021, DeMars et al. 2023), underscoring the importance of both the extent and duration of anthropogenic features on the landscape. On average, roads and other linear features represented more than half of human disturbance across all caribou ranges in Ontario between 2010-2013, and more than half of the total disturbance in southern caribou ranges where management disturbance thresholds under the Species at Risk Act are also often exceeded (MNRF 2014a-i, ECCC 2020). Direction for caribou habitat in the Forest Management Guide for Boreal Landscapes (2014) emphasizes the timely decommissioning of operational roads and regeneration of linear disturbances following harvest. However, the effectiveness of such measures in contributing to caribou conservation outcomes remains uncertain. The Ontario-Canada scientific assessment (ECCC 2024) highlights significant limitations in understanding how individual management actions related to habitat disturbance and restoration, contribute to population-level outcomes, noting insufficient information to evaluate how policies are implemented or how consequential they are in practice. More broadly, restoration of linear features such as roads, is understood to require decades before functional recovery for caribou occurs, and empirical evidence linking these interventions to reduced predation risk or improved population persistence remains limited in Ontario. In this context, while policy direction calls for rapid decommissioning and regeneration of road networks, there is limited empirical evidence demonstrating the frequency, effectiveness,

or population-level benefits of these actions in Ontario, and their role in limiting predator access remains an important but unresolved area of uncertainty.

Understanding the extent to which regeneration of linear features is sufficient to restore functional habitat, and identifying the specific site characteristics and time needed to restore function, are central to linking site-level management actions to landscape-level conservation goals. From a caribou perspective, functional restoration involves substantially reducing the movement, access, and resource advantages created by a road so that use by predators and prey relevant to caribou risk approaches surrounding forest conditions. Ontario's Integrated Range Assessment Protocol recognizes that older, regenerated linear features may no longer have a discernable effect and indicates that linear features thought to be benign to caribou should be omitted to ensure accurate disturbance estimates (MNRF, 2014a). However, lack of data on the condition of linear features and clearly defined and defensible criteria to identify when linear features are functionally restored challenge implementation (J. Shuter and K. Green, pers. comms.).

The context-dependent nature of relationships between linear features and space use of caribou predators and their prey (e.g., functional responses in habitat selection) creates challenges for identifying general management or restoration targets (Ray 2014; Dickie, Love et al. 2023). Accurate estimation of road densities first requires an understanding of when a road continues to function as a disturbance from a caribou perspective. A literature review by Dickie et al. (2023) to identify evidence-based management targets for linear feature management found that most studies focused on how linear features influence space use by caribou, their predators and their primary prey, with little evidence for clear thresholds in relationships upon which to base management targets. Previous recommendations to combine restoration of vegetation structure with measures that reduce early-seral vegetation and impede movement on linear features (Bentham and Coupal 2015, Ray 2014) are supported by more recent studies.

Use of linear features by boreal caribou predators and their primary prey linked to ease of movement and available forage supports recommendations that restoration combine techniques that impede movement of wildlife and humans with vegetative restoration (Tattersall et al. 2023). However, evidence of caribou, predators and their primary prey responses to restoration focused on blocking linear features and restoring vegetation has been variable (e.g., Keim et al. 2019, Dickie, Serrouya, DeMars et al. 2017, Tattersall et

al. 2020, Dickie et al. 2021, Dickie, Sherman et al. 2023). Notably, most research examining wildlife use of linear features and functional restoration criteria for boreal caribou conservation has taken place in western Canada (but see Benoit-Pépin et al. 2024, Kittle et al. 2017, and Newton et al. 2017), where restoration has received the greatest attention in response to high cumulative disturbance, continuing development pressure, and extensive monitoring that has documented low probabilities of self-sustaining local populations (Ray 2014).

Road effects on caribou are mediated through a broader mammal community. Predators and prey respond to roads under different seasonal, habitat, access, and behavioural conditions, and these responses can alter the species interactions through which industrial disturbance affects caribou (Curveira-Santos et al. 2024). A caribou-focused assessment of restoration therefore requires examining whether roads continue to support use by this broader community and treating vegetation condition and single-species responses as partial indicators. Comparing road use with forest reference conditions provides an indirect basis for evaluating whether caribou-relevant road function is diminishing. Direct effects on caribou survival, recruitment, and population persistence require other forms of evidence.

Objectives

Our study investigated factors that influence use of forestry roads across a gradient of regeneration by mammals that directly and indirectly affect boreal caribou. We compared their use of roads with baseline use in the surrounding forest to evaluate continued road function relevant to caribou conservation and to support the development of functional road restoration guidance.

We collected and analyzed data from a multi-year camera trap survey conducted along forestry roads, both those that remain open and maintained for use by industry and those than have been closed and left to regenerate naturally, across caribou habitat within three ranges in northwestern Ontario. Because active decommissioning was uncommon in the region, we focused on abandoned roads, but included sites with berms, scarification, water crossing removals, and/or seeding/planting to limit human use and promote revegetation where encountered. The study therefore assessed roads across

gradients of regeneration, access, and road condition rather than experimentally comparing decommissioning treatments. We then compared use intensity on non-primary roads to that of forest reference sites to inform functional road restoration guidance from a caribou perspective.

Mammal communities broadly affect boreal caribou directly and indirectly through predator-prey and intraguild interactions influenced by industrial disturbance (Curveira-Santos et al. 2024). Caribou habitat selection reflects efforts to minimize predation risk while securing forage and suitable conditions for reproduction (McGreer et al. 2015; Hornseth and Rempel 2016). Applying this disturbance-mediated community effects framework through a boreal caribou lens, we used a model selection approach to identify factors that influence use intensity of forestry roads by five focal mammal species selected for their direct or indirect relevance to boreal caribou conservation: wolf (*Canis lupus*), black bear (*Ursus americanus*, herein bear), moose (*Alces alces*), Canada lynx (*Lynx canadensis*, herein lynx), and snowshoe hare (*Lepus americanus*, herein hare). For each species, we compared models representing four mechanistic a priori hypotheses that road use intensity is influenced by: 1) ease of movement, 2) risk avoidance, 3) human disturbance, and 4) resource availability. We then modelled use intensity on non-primary roads alongside use in the forest to assess whether, and under what conditions, road use approached forest reference levels.

Our approach identifies candidate indicators of functional restoration and the considerations needed to translate them into defensible criteria and thresholds. These indicators assess whether roads continue to support use by mammals that directly and indirectly affect caribou and therefore whether they retain ecological functions relevant to caribou conservation. They do not directly measure effects on caribou survival, recruitment, or population persistence. Rather, they are intended to support the development and evaluation of road decommissioning and restoration strategies in landscapes managed for caribou conservation in Ontario.

Our study informs four conservation measures across three themes outlined in the Agreement for the Conservation of Caribou, boreal population, in Ontario:

1.3 Assessment of the effectiveness and efficiency of habitat restoration approaches in contributing to self-sustaining local populations and managing cumulative

disturbance at a range scale and application of the recommendations of the assessment.

3.1 Continue to integrate the direction in the Forest Management Guide for Boreal Landscapes into forest management plans that intersect with ranges and review forest management guide direction to assess the effectiveness of existing direction in supporting the shared outcome of self-sustaining local populations.

4.1 Refine existing evidence-based approaches to manage for self-sustaining local populations in ranges and integrate them into provincial and federal boreal caribou conservation frameworks, where appropriate.

4.2 Ontario and Canada to review updated relevant information (e.g., monitoring, science/research) as it is generated under the agreement and consider adoption into federal and provincial boreal caribou conservation policies and approaches.

Methods

Study area

The study took place in caribou habitat across an approximately 6,000 km2 area surrounding the municipalities of Red Lake and Ear Falls, Ontario, on traditional Anishinabewaki territory, part of Treaty 3 lands, and the homeland of the Michif Piyii (Métis) (Fig. 1). The study area spans parts of the Red Lake and Trout Lake managed forests in the Area of Undertaking. It is located to the east of Woodland Caribou Provincial Park and overlaps the Churchill, Sydney and Berens caribou ranges.

The area is in the boreal shield ecozone and Lake Wabigoon Ecoregion (4S) where the climate is relatively cool and dry (Crins et al. 2009). In this ecoregion, mean annual temperatures range between 0.1-2.6°C and mean annual precipitation between 565-724 mm (Crins et al. 2009) with mean summer rainfall between 245-291 mm (Mackey et al. 1994, 1996). Forests dominate the landscape (65%) comprising mixed forest (25%), sparse forest (24%), coniferous forest (14%) and deciduous forest (2%). Cutovers cover 5% and water covers 24% of the ecoregion (Crins et al. 2009). Stand replacing fires in upland conifer forest cycle between 50-187 years, whereas those in mixed forests

vary in intensity and cycle between 63-210 years (Crins et al. 2009, van Sleeuwen 2006). Flora and fauna in the area are typical of boreal ecosystems with jack pine, black spruce, balsam fir, trembling aspen, white birch, and some white spruce in upland sites, and black spruce, tamarack, black ash, and balsam poplar in lowland habitats. Terrestrial boreal mammal species in the area expected to directly and indirectly affect boreal caribou include wolf, coyote (*Canis latrans*), black bear, Canada lynx, wolverine (*Gulo gulo*), moose, white-tailed deer (*Odocoileus virginianus*), beaver (*Castor canadensis*), snowshoe hare, and red squirrel (*Tamiasciurus hudsonicus*).

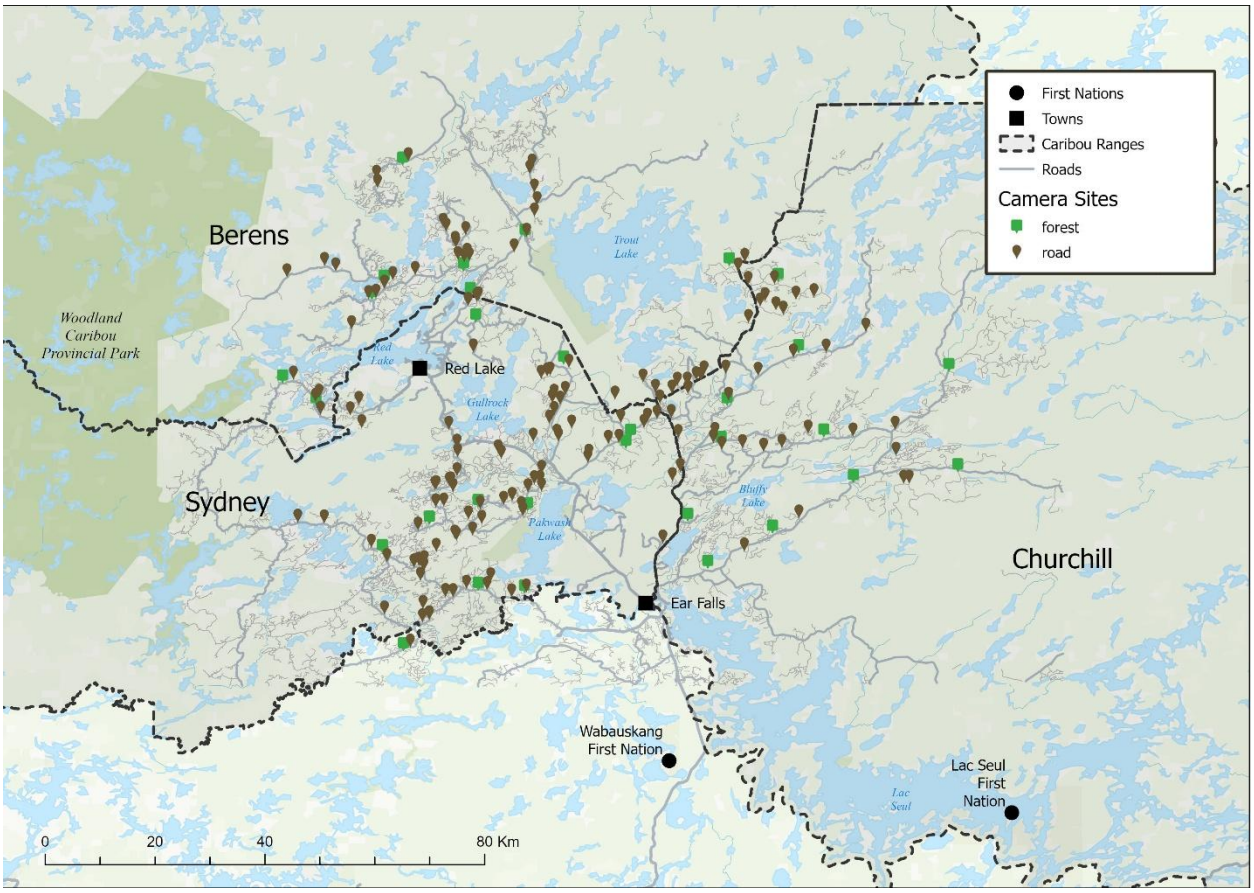

Figure 1. Camera-trapping survey on forestry roads within Sydney, Churchill and Berens caribou ranges spanning a gradient of regeneration in northwestern Ontario, Canada.

Forestry, including cutblocks and linear infrastructure, has been the dominant source of anthropogenic disturbance in the broader landscape since the late nineteenth century (Crins et al. 2009; Racey and Armstrong 2000). Mining exploration and development are an increasing presence in this high-grade gold district, with several mines and

proposed projects at different stages of development, including Red Lake Operations, Madsen Gold Mine, the Great Bear Gold Project, and the Springpole Gold Project. These activities have increasingly required access for exploration, construction, operation, and maintenance, potentially creating new roads, upgrading existing forestry roads, and extending the duration and intensity of traffic within the road network.

The forestry road network also supports extensive fishing, hunting, trapping, and motorized recreation. Numerous lodges and hunt camps are accessed by these roads, with fishing focused mainly on walleye and northern pike and hunting focused mainly on moose and bear. Lodge operators may maintain otherwise unmaintained roads, establish and service bear-baiting sites, and use all-terrain vehicles to reach hunting and fishing areas. Some roads are also plowed by local residents during winter, while snowmobiles and all-terrain vehicles allow continued access where roads are no longer maintained for forestry. Camera records from this study documented road maintenance, vehicle traffic, and access associated with these activities. Together, these uses can prolong the functional life of forestry roads and maintain human access and disturbance after their original industrial purpose has declined.

Field and spatial data collection

Between December 2018 – April 2021 and September 2024 – October 2025, we deployed Reconyx HyperFire Professional Series camera traps at 175 sites on forestry roads encompassing a gradient of regeneration stages and at 32 sites in the forest as reference sites for estimating baseline use away from the physical road corridor. We sampled roads that were maintained and unmaintained including, primary, secondary, and operational roads. Road sites were generally selected randomly from the Ontario Road Network (ORN) Road Net Element database. However, to ensure our sampling captured road sites across a full gradient of regeneration stages, we set cameras on a subset of road segments randomly selected from a database of abandoned roads supplied by the Ontario Ministry of Natural Resources and Forestry (OMNRF). We also targeted sites where active decommissioning (e.g., berms, scarification, water crossing removal, planting/seeding) had been implemented (M. Smith, pers. comm.) and where there appeared to at least some vegetation regeneration based on our on-the-ground observations. These measures varied among sites and were not sampled through an

experimental treatment design. In addition, a small number of road sites were intentionally selected by field crews based on roads with more advanced vegetation regeneration to ensure adequate sampling of this end of the regeneration gradient. Forest sites were randomly selected using the create random points tool in ArcGIS Pro across the study area within a 500 m buffer around roads for accessibility while ensuring a minimum distance of 50 m to the nearest road.

We deployed cameras approximately 1 m above ground level on trees with an unobstructed view and diameter at breast height of at least 12 cm, angled downward to provide a clear view of wildlife travelling on roads or trails in accordance with the Ontario Wildlife Monitoring network camera trap protocol (Dupee et al. 2021). We cleared surrounding vegetation to minimize false triggers and, where possible, cameras were set facing north to optimize image quality. A plastic shield was affixed to the tree above the camera to prevent snow from accumulating on the camera during winter. We programmed cameras to take a rapid burst of 3 photographs for each motion detected and timelapse photos once every 1-24 hours depending on the camera model. We analyzed images using Timelapse software (Greenberg et al. 2019, https://timelapse.ucalgary.ca), recording the species and number of individuals in each frame. When species identification was uncertain, images were analyzed by at least two individuals.

At each road site, we assessed movement speed and visibility on the road relative to the forest, documented forage species, and recorded vegetation heights for validating LiDAR. We measured the walking speed of one individual on and off the road over 50 m. A single observer estimated percent hiding cover at two heights, 0.5 m and 1.5 m, for a 65 cm wide by 125 cm high white screen at 15 m in two directions each, to assess relative visibility on/off the road. Two observers surveyed a rectangular 100 m2 plot on the road at each site and recorded plant species, the tallest height observed for each species, and estimated percent cover of bare ground, rocks, moss and litter combined, lichen, fungi, graminoids, forbs, shrubs, trees < 5 m tall, and trees > 5 m tall. The same data were collected at forest sites, except that vegetation plot sampling occurred in the forest rather than on a road and walking speed and hiding cover were only measured in the forest.

We estimated mean vegetation height and coefficients of variation over 100 m at each road and forest site (50 m on either side of the camera location) from the Forest

Resources Inventory leaf on LiDAR Canopy Height Model. LiDAR data was validated by evaluating the relationship between mean LiDAR-derived heights and the tallest height measured in the field for each 100 m2 vegetation plot (Fig. A1). Forest age was estimated as the mean value within a 100 m radius using the NTEMS Forest Age dataset. We estimated the distance to the nearest water source from the Ontario Integrated Hydrology dataset. As measures of human activity, we estimated distance to primary roads using the Ontario Road Network Road Net Element database and distance to active mines from the Principal Mineral Areas, Producing Mines, and Oil and Gas Fields (900A) dataset. All geospatial data were extracted with ArcGIS Pro v 3.5.4.

Although we did not handle or capture wildlife, we obtained a Wildlife Scientific Collector's Authorization from the Ontario Ministry of Natural Resources (No. 1106474) for the 2024-2025 camera trap survey. As part of this process, the Ontario Ministry of Natural Resources notified Wabauskang and Lac Seul First Nations of our study. We reached out to these communities ourselves and other communities in the surrounding area, as well as to tribal councils, to share information about the project and the locations where cameras were set.

Caribou-focused analytical framework

We treated road use by focal mammals as an indicator of whether forestry roads retained ecological functions relevant to caribou conservation. The five focal species represented predator, alternate-prey, and intraguild pathways through which industrial disturbance can directly and indirectly affect caribou (Curveira-Santos et al. 2024) and were detected frequently enough for species- and season-specific modelling. Road use intensity was the measured response, while road vegetation, travel conditions, resource availability, human activity, and detections of other focal mammals represented potential mechanisms influencing that response.

Forest sites provided reference conditions without the physical road corridor. We treated road use approaching forest reference levels as evidence consistent with diminishing road function, while recognizing that similar or low use intensity could also arise from poor habitat quality, avoidance of human activity, or other ecological and disturbance conditions. The analysis therefore identifies candidate indicators of functional restoration

and considerations for translating them into defensible criteria and thresholds. It does not directly estimate effects on caribou survival, recruitment, or population persistence.

Identifying drivers of road use by focal mammals

We fit models and performed model selection to identify factors that influenced road use intensity for five boreal mammals selected because they directly and indirectly affect boreal caribou through predator-prey and intraguild interactions influenced by industrial disturbance (Curveira-Santos et al. 2024), and were detected frequently enough in the study area for species- and season-specific modelling: wolf, bear, moose, lynx, and hare.

Data quality and model variables

Data quality control measures were taken prior to fitting models. We only retained data from cameras that operated for at least 25 consecutive days (Hamel et al. 2013). For cameras operating between 2019-2021, we pooled data from cameras set within 500 m of each other on the same road segment. When this occurred, cameras typically were not deployed during overlapping periods. However, when this did occur, we verified that observations were not duplicated across cameras prior to pooling data and found no instances where duplicate observations were observed. For 2024-2025, cameras were set a minimum of 1 km apart for spatial independence. Following quality control measures, camera trap data were retained for 152 road camera sites, and 32 forest sites. The road sites retained were monitored for 243 days on average (median = 312 days, min = 29 days, max = 846 days), and forest sites were monitored for an average of 337 days (median = 342 days, min = 139 days, max = 371 days). We considered observations occurring at least 30 minutes apart as independent events (Smith 2025, Lepard et al. 2018) and retained the observation with the highest number of individuals in a single frame with a 30-minute period.

Model fitting and selection

We fit species-specific models separately for snow-on (November – April) and snow- off (May – October) seasons. We modelled distributions for each species- and season-specific model based on the assumed distribution for null models that ranked highest using Akaike's Information Criterion (AIC) corrected for small sample sizes (Hurvich and

Tsai 1989). For each species and season, we tested linear and quadratic parametrizations of the negative binomial distribution (Hardin and Hilbe 2007) and the Poisson distribution, with and without zero-inflation for each distribution. When zero-inflated and non-zero-inflated distributions were indistinguishable, we selected the simpler non-zero-inflated distribution. Negative binomial distributions with a linear parameterization were among the highest ranked for all species and seasons except moose in the snow-on season, for which the quadratic parameterization ranked highest; zero-inflated distributions ranked highest for moose and hare in the snow-off season. Use intensity for bear was only modelled for the active snow-off season. We assessed pairwise correlations among continuous predictor variables prior to fitting models to exclude one variable when $r > 0.7$; however, no correlations meeting this criteria occurred. We standardized all continuous predictor variables. See Tables A1-A3 in the Appendix for additional information on the complete candidate model set. Models were fit using the glmTMBB package (McGillycuddy et al. 2025, Brooks et al. 2017) and model fits assessed with the dHARMA package (Hartig 2026). We assessed multicollinearity among predictor variables for fitted models using the performance package (Lüdecke et al. 2021), retaining those with VIF <3 (Zuur et al. 2010). We ranked candidate models with AIC using the MuMIn package (Barton 2026) and estimated conditional and marginal effects with the performance package. All analyses were performed in R v 4.4.1.

Comparison with forest reference conditions

We compared predicted use intensity of non-primary roads and forest sites for predictors identified to influence road use in the above model selection analysis to identify candidate indicators of functional restoration and considerations for developing guidance. Primary roads that were included in the above analysis were excluded in the current analysis because they were open and actively maintained and therefore were not considered candidates for functional recovery under current conditions.

We fit generalized linear mixed effects models predicting use intensity for highest-ranked models for each species and season, adding a site type variable to distinguish road and forest sites. We limited the number of parameters in these models by only including fixed effect variables from highest-ranked models with statistically significant coefficients. We

replaced categorical measures of vehicle traffic frequency (daily, weekly, monthly, <monthly, none) with a binary variable reflecting whether vehicle traffic was observed or not. We additionally replaced relative measures for walking speed and hiding cover at road sites with absolute measures that could be directly compared to measures taken at forest sites. Random intercepts for site ID and road ID for the nearest primary road were also retained in these models. In these models LiDAR-derived mean vegetation height and coefficients of vegetation height were highly correlated (>0.7), and as such in models where both parameters would have been included, only mean vegetation height was retained.

We interpreted convergence in predicted use between non-primary roads and forest reference sites as evidence consistent with diminishing road function. We considered the habitat, access, and disturbance conditions associated with convergence because similar use levels could arise through mechanisms other than functional recovery.

Key Findings and Implications

Together, the analyses addressed two linked questions: whether regenerating forestry roads remained functionally distinct from surrounding forest for mammals that directly and indirectly affect caribou, and which road, access, seasonal, and landscape conditions were associated with that distinction. We integrated the road-use models, comparisons with forest reference sites, road-condition measurements, and camera detections to interpret both the persistence of road function and its implications for functional restoration.

The results are organized around five main findings. We begin with the overall pattern of road and forest use across the focal mammal community, then examine the mechanisms and conditions associated with continued road use, including ease of movement and motorized access. The later sections consider how similar road and forest use should be interpreted and how season and landscape position affect the significance of the findings for caribou conservation and restoration planning.

Regenerating forestry roads generally remain functionally distinct from forest across the focal mammal community

Road–forest differences were strongest and most consistent during snow-off

Overall, the five focal mammals used non-primary roads spanning a gradient of regeneration stages more than forest reference sites, although the magnitude of the difference varied across species and seasons (Tables A9–A13). During the snow-off season, daily detections at forest sites were significantly lower, by 0.7 to 3 counts on average, compared with non-primary road sites across species (Tables A9–A13). All five focal species used non-primary roads more than forest reference sites during the snow-off season, indicating that roads across the sampled regeneration gradient generally retained ecological functions distinguishing them from forest.

The persistence of the road effect varied among species and seasons

Although wolf road-use intensity was higher during the snow-off season, its relative use of roads compared with forest sites increased during the snow-on season, and the road–forest difference was statistically significant in both seasons (Table A9). Use intensity of non-primary roads also remained higher than forest sites for moose, lynx, and hare during the snow-on season, although the differences were not statistically significant for moose and lynx and were marginal for hare (Tables A10–A12).

Across snow-on and snow-off seasons, site type, non-primary road or forest, influenced predicted use intensity for moose to a similar extent. Effects of site type on predicted use intensity for lynx and hare decreased severalfold during the snow-on season. Bear use was modelled only during its active snow-off season. Together, these findings show that the magnitude and seasonal persistence of the road effect differed across the focal mammal community.

Community-level responses provide the basis for assessing road restoration from a caribou perspective

Our study finds that wildlife of importance to caribou conservation respond to forestry roads in different ways, emphasizing the complexity of restoring roads from a caribou perspective. Mammal communities broadly affect boreal caribou directly and indirectly through predator-prey and intraguild interactions influenced by industrial disturbance (Curveira-Santos et al. 2024).

In Ontario, wolves are the primary predator of caribou, while their diet consists mainly of ungulates, including moose (Popp et al. 2018). Disturbance in caribou habitat replaces mature old growth with early-seral forest, supporting higher densities of wolf primary prey and, in turn, higher wolf densities that increase caribou predation risk (Serrouya et al. 2021, Wittmer et al. 2005). Other predators, including bear and lynx, also prey on caribou, predominantly calves (Huang et al. 2021, Wehr et al. 2025). Consequently, prey such as hare that support subordinate predators and also respond to human disturbance have the potential to affect caribou predation risk (Curveira-Santos et al. 2024). The five focal species therefore represent direct predation, alternate-prey, and broader predator-prey and intraguild pathways through which roads can remain relevant to caribou conservation. Considering these pathways together is consistent with community-focused approaches that assess ecological responses across interacting species rather than through a single-species lens (Brown et al. 2021).

Restoration implications

Our findings highlight that restoration from a caribou perspective requires approaches that consider the broader animal community and prioritize functional outcomes for mammals that directly and indirectly affect caribou. Functional road restoration should therefore be evaluated by assessing whether use by a suite of focal mammals representing these pathways approaches the range observed at appropriate forest reference sites, while promoting ecological restoration toward caribou habitat that contributes to supporting self-sustaining populations.

The study provides the rationale and initial evidence for this community-level endpoint. Defining suitable forest reference ranges and numerical decision thresholds, and linking

these indicators to caribou survival, recruitment, and population persistence, require additional work.

These community-level differences are best understood by examining the road characteristics and conditions that continue to provide movement, visibility, or resource advantages relative to forest.

Ease of movement is the primary mechanism maintaining road function, with additional road characteristics shaping species-specific use

Ease of movement was the most consistent driver of road use

Ease of movement was the most consistently supported driver of road use across the focal mammals. Variables associated with ease of movement occurred in all highest-ranked models across species and seasons, often with larger effect sizes that were statistically significant (Table 1; Tables A4–A8). Human disturbance and resource availability were also important, although they were represented less consistently among the highest-ranked models and statistically supported effects. The common pattern was continued use of roads as movement corridors, while the road and landscape characteristics associated with that use differed among species and seasons.

Roads continued to provide travel, visibility, and vegetation-mediated advantages

Travel efficiency

Use by wolves, bears, moose, and lynx was associated with one or more road characteristics that facilitate movement, including shorter vegetation, faster walking conditions, and relatively open or uniform corridors. During the snow-off season, wolves used roads that allowed faster travel relative to the forest more, although this effect was not statistically significant. Bears used roads that allowed faster travel and had shorter vegetation. In both snow-on and snow-off seasons, moose used roads more where vegetation was shorter and walking speeds were faster than in the surrounding forest.

Lynx used roads with shorter vegetation of relatively consistent height, which maintained open travel corridors (Tables A4–A7).

Ease of movement was therefore the most common factor influencing use across species and seasons. All species except hare used roads with characteristics that facilitate movement across the landscape. Regenerating roads may also provide both forage and movement advantages for moose. Moose used roads more where graminoid cover was higher during snow-off and where shorter vegetation and faster walking conditions facilitated travel across seasons (Loosen et al. 2021). These results are consistent with studies showing that regeneration and road characteristics shape the movement and use of linear features by large mammals (Finnegan et al. 2018; St-Pierre et al. 2022).

Table 1. Highest-ranked models of forestry road use intensity by species and season using Akaike's Information Criterion corrected for small sample size (AICc). Models are based on four hypothesized drivers of use intensity: ease of movement (move), risk avoidance (risk), human disturbance (dist), and resource availability (res). Number of parameters (k), difference in AIC score with the highest-ranked model (ΔAIC), Akaike weight (AICcWt), log-likelihoods (LL), and variation explained by fixed effects (marginal R2) and fixed and random effects (conditional R2) are included for each model. All models included random intercepts for camera site (1| site_ID) site and nearest primary road (1| nearest_primary_ID). Models within ΔAICc < 2 of highest-ranked models are shown. See Tables A1-A3 in the Appendix for additional information on the complete candidate model set

species	season	hypotheses	model	k	AICc	ΔAICc	AICcWt	LL	marginal R^2	conditional R^2
wolf	snow-on	move + dist	mean_height + cv_height + rel_speed + rel_cover0.5 + mine + primary + human_activity	14	3051.416	0	0.526874	-1511.7	0.271	0.397
		move + risk + dist	mean_height + cv_height + rel_speed + rel_cover0.5 + lynx + mine + primary + human_activity	15	3052.385	0.969036	0.324551	-1511.18	0.271	0.396
	snow-off	move + risk	mean_height + cv_height + rel_speed + rel_cover0.5 + lynx + bear	10	3614.551	0	0.366375	-1797.27	0.187	0.471
		move	mean_height + cv_height + rel_speed + rel_cover0.5	8	3614.711	0.159551	0.338283	-1799.35	0.187	0.473
		move + risk + dist	mean_height + cv_height + rel_speed + rel_cover0.5 + lynx + bear + mine + primary + human_activity	16	3616.431	1.879828	0.143129	-1792.2	0.223	0.488
moose	snow-on	res + move	forest_age + water + lichen + shrub + sapling + mean_height + cv_height + rel_speed + rel_cover1.5	13	2508.251	0	0.526004	-1241.12	0.165	0.332
	snow-off	res + move + risk + dist	forest_age + water + graminoid + forb + shrub + sapling + mean_height + cv_height + rel_speed + rel_cover1.5 + wolf + lynx + bear + mine + primary + human_activity	23	4307.36	0	0.350198	-2130.64	0.135	0.245
		move + risk + dist	mean_height + cv_height + rel_speed + rel_cover1.5 + wolf + lynx + bear + mine + primary + human_activity	17	4307.52	0.160575	0.323181	-2136.74	0.107	0.243
		res + move + risk	forest_age + water + graminoid + forb + shrub + sapling + mean_height + cv_height + rel_speed + rel_cover1.5 + wolf + lynx + bear	17	4308.587	1.227574	0.189561	-2137.27	0.114	0.243
bear	snow-off	res + move + risk + dist	forest_age + water + hare + moose + forb + mean_height + cv_height + rel_speed + rel_cover0.5 + wolf + lynx + mine + primary + human_activity	21	8711.967	0	0.654216	-4334.95	0.107	0.234
		move + risk + dist	mean_height + cv_height + rel_speed + rel_cover0.5 + wolf + lynx + mine + primary + human_activity	16	8713.52	1.553442	0.300881	-4340.74	0.096	0.230
lynx	snow-on	res + move + dist	forest_age + water + hare + moose + mean_height + cv_height + rel_speed + rel_cover0.5 + mine + primary + human_activity	18	3936.237	0	0.621625	-1950.1	0.189	0.397
		res + move + risk + dist	forest_age + water + hare + moose + mean_height + cv_height + rel_speed + rel_cover0.5 + wolf + mine + primary + human_activity	19	3938.067	1.829934	0.248979	-1950.01	0.189	0.397
	snow-off	res + move + risk + dist	forest_age + water + hare + moose + mean_height + cv_height + rel_speed + rel_cover0.5 + wolf + bear + mine + primary + human_activity	20	4593.601	0	0.380706	-2276.77	0.084	0.279
		move + risk + dist	mean_height + cv_height + rel_speed + rel_cover0.5 + wolf + bear + mine + primary + human_activity	16	4593.719	0.117787	0.358932	-2280.84	0.080	0.276
hare	snow-on	res + move + dist	forest_age + water + shrub + sapling + mean_height + cv_height + rel_speed + rel_cover0.5 + mine + primary + human_activity	19	13215.36	0	0.769079	-6588.66	0.326	0.549
		res + move + risk + dist	forest_age + water + shrub + sapling + mean_height + cv_height + rel_speed + rel_cover0.5 + wolf + lynx + mine + primary + human_activity	21	13218.92	3.553304	0.130131	-6588.44	0.326	0.550
	snow-off	move + dist	mean_height + cv_height + rel_speed + rel_cover0.5 + mine + primary + human_activity	14	8683.723	0	0.309196	-4327.85	0.21	0.570
		move + risk + dist	mean_height + cv_height + rel_speed + rel_cover0.5 + wolf + lynx + bear + mine + primary + human_activity	17	8684.198	0.474619	0.243877	-4325.08	0.211	0.57
		move	mean_height + cv_height + rel_speed + rel_cover0.5	8	8684.726	1.002449	0.187307	-4334.36	0.165	0.564
		move + risk	mean_height + cv_height + rel_speed + rel_cover0.5 + wolf + lynx + bear	11	8685.04	1.316245	0.160109	-4331.51	0.167	0.563

Visibility and hunting opportunity

Roads with higher visibility relative to the surrounding forest were used more by wolves during winter, lynx during summer, and bears during the snow-off season. Greater visibility, combined with faster travel, could increase hunting opportunity by allowing predators to move efficiently and detect prey along the road corridor. Direct observations of wolves hunting ungulates on linear features provide further evidence that these corridors can function as hunting infrastructure (Gable et al. 2023).

Vegetation-mediated forage and cover

Vegetation structure and composition influenced species in different ways. Moose used roads more where graminoid cover was higher during the snow-off season. Lynx used roads more in younger forests, where hare habitat was also more prevalent, and where shorter vegetation of relatively consistent height maintained an open corridor. Hare used roads in young forest habitat during the snow-on season and used roads with taller vegetation that provided more cover during the snow-off season. Such responses are consistent with the importance of dense understory and early-seral cover to snowshoe hare habitat use (Litvaitis et al. 1985; St-Laurent et al. 2008; Bois et al. 2012). These findings show that roads can simultaneously provide movement, forage, and cover functions, with their importance varying among species and seasons.

Candidate indicators produced different patterns of convergence with forest across species

Identifying potential indicators for establishing functional restoration criteria presented challenges because site-level measures influencing use intensity across non-primary roads and forest sites varied among species and seasons. Generally, predicted use intensity of non-primary roads approached levels more similar to forest sites when conditions became less suitable for particular species in relation to ease of movement and available resources.

When vegetation was taller, use intensity for bears during the snow-off season and lynx during the snow-on season decreased, approaching levels observed at forest sites (Fig. 2). Conversely, hare use intensity during the snow-off season increased and diverged

between non-primary road and forest sites as vegetation became taller (Fig. 2). Roads with slower walking speeds experienced lower use intensity by bears during the snow-off season and moose during the snow-on season, although differences in moose use intensity between non-primary road and forest sites were not statistically significant (Fig. 2).

Moose use intensity increased and diverged between non-primary road and forest sites with higher graminoid cover during the snow-off season (Fig. 3). Lynx use intensity on non-primary roads decreased during the snow-off season when hiding cover was high, approaching that of forest sites (Fig. 3). Lynx and hare used younger forests more during the snow-on season, and levels of use were comparable between non-primary road and forest sites (Fig. 3).

The same vegetation change could therefore have different implications across the focal community. Taller vegetation was associated with road use approaching forest levels for bear and lynx, while hare use increased and diverged further from forest under taller vegetation conditions. Higher graminoid cover also increased the divergence in moose use between roads and forest. These contrasting responses prevent vegetation height or another single physical measure from serving as a universal indicator of functional recovery.

Our findings align with previous studies that have proposed vegetation height (Dickie, Serrouya, McNay et al. 2017), walking speed (Keim et al. 2019), and visibility (Benoit-Pépin et al. 2024) as measures for assessing functional restoration based on observed effects on the use intensity and movement speeds of caribou predators and their alternate prey. No single measure of vegetation characteristics explained use across species in our study. Because different species responded to different features, relying on selected vegetation targets alone is unlikely to functionally restore roads for caribou.

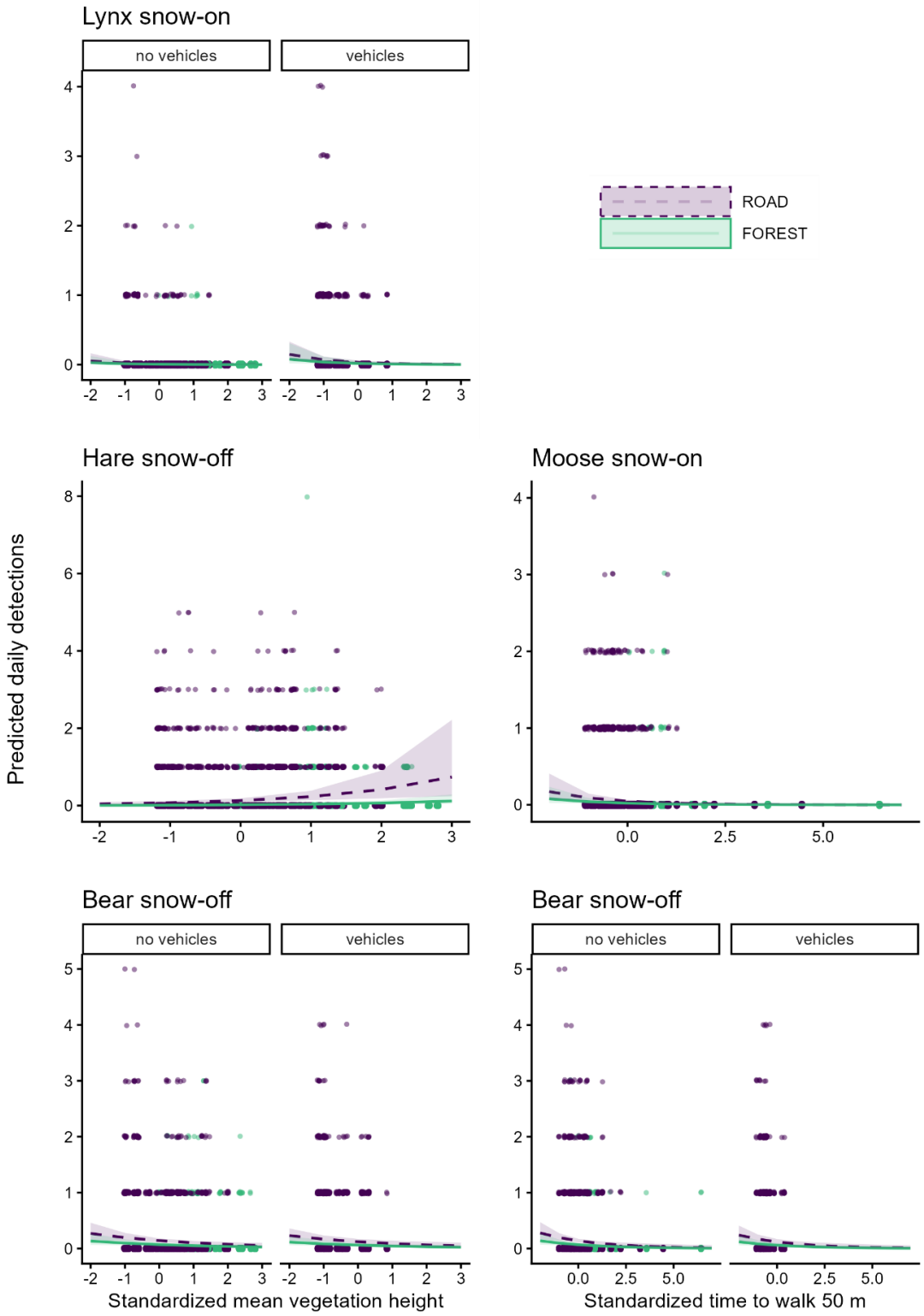

Figure 2. Non-primary road and forest use intensity predicted based on mean vegetation height (left) and walking speed (right).

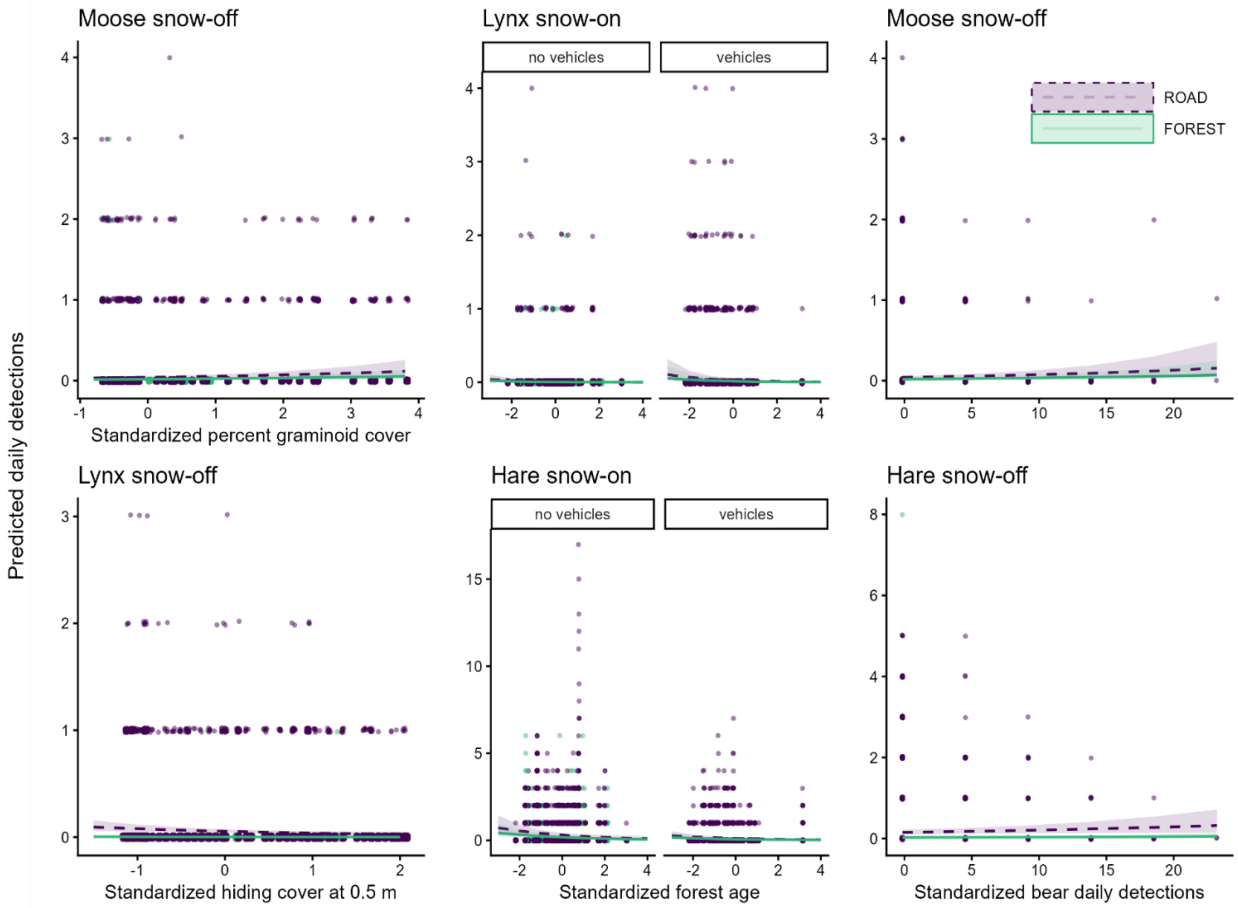

Figure 3. Non-primary road and forest use intensity predicted based on graminoid cover (upper left), hiding cover (bottom left), forest age (center), and bear daily detections (right).

Restoration implications

Vegetation recovery should focus on obstructing physical travel, reducing long sightlines and graminoid dominance, promoting woody regeneration and structural complexity, and breaking up the continuity of the open travel corridor. These physical and vegetation characteristics can serve as candidate indicators of whether a road continues to provide movement, visibility, forage, or cover advantages. They also provide practical targets for restoration treatments.

The effectiveness of those treatments should be evaluated through functional outcomes by comparing road use by focal mammals with the range of use observed at appropriate forest reference sites. Vegetation and road-condition measures describe the restoration

treatment and trajectory. Wildlife use relative to forest conditions provides the stronger measure of functional outcome.

The study identifies directions for vegetation recovery and physical obstruction, but it does not establish a single vegetation-height, hiding-cover, walking-speed, or graminoid-cover threshold that defines functional recovery. Defensible criteria will require several indicators to be assessed together and interpreted across the focal mammal community.

Motorized access can maintain movement advantages and slow vegetation recovery, making year-round access control a separate and essential component of functional road restoration.

Vehicle access maintains conditions that support movement and delays functional restoration

Responses to vehicle traffic varied among species and seasons

Vehicle traffic increased road use by wolves across both seasons, with the effect of vehicle traffic being greater during the snow-on season, when lynx also used roads with vehicle traffic more than those without it. During the snow-on season, vehicle traffic that facilitated movement was the strongest predictor of use for both wolves and lynx (Tables A4 and A5). When there was no snow, wolves continued to use roads with vehicle traffic more, although the effect was not statistically significant in the road-use driver model (Table A4).

Vehicle traffic significantly increased predicted use intensity for wolves in both seasons and for lynx during the snow-on season, leading to greater divergence from use intensities observed at forest reference sites (Fig. 4; Tables A9 and A11).

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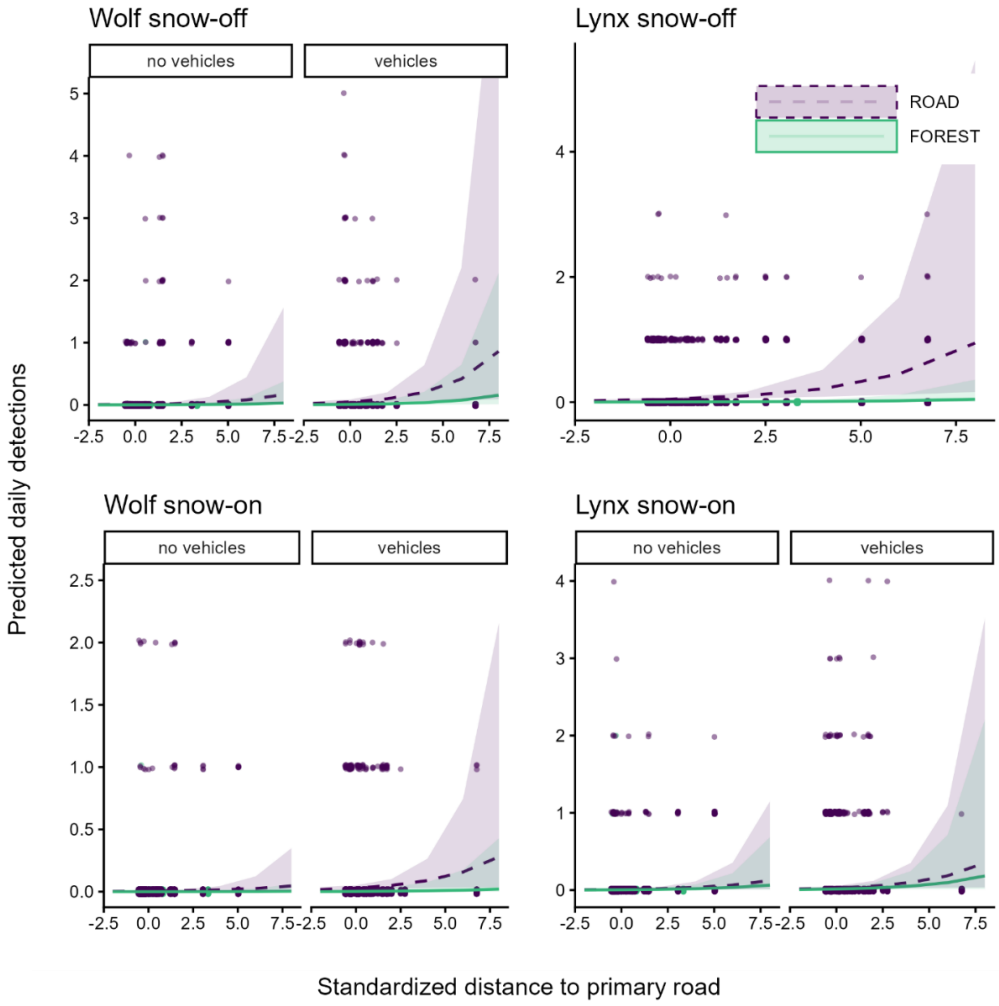

Figure 4. Predicted use intensity of non-primary roads and forest reference sites for wolf (left) and lynx (right) during snow-off (upper) and snow-on (lower) seasons in relation to distance to the nearest primary road. Panels distinguish the presence and absence of vehicle traffic where vehicle activity was retained in the model.

Responses differed among the other focal species. Bears used roads with vehicle traffic less during the snow-off season, and hare avoided roads with more frequent vehicle traffic during the snow-on season (Tables A6 and A8). Moose road use was unaffected by vehicle traffic in either season (Table A7). Vehicle access therefore affected focal

mammals differently, while the increased use by wolves across seasons and by lynx during winter is particularly relevant to road function from a caribou perspective.

Vehicle traffic maintained conditions that facilitate movement

Snow affects wildlife movement, energetic costs, access to forage, and species interactions (Fancy and White 1987, Crête and Larivière 2003, Droghini and Boutin 2018, Peers et al. 2020, Beaupré et al. 2026). Snowpack properties determine the degree to which animals sink into the snow, influencing movement ability and energetic costs (Sullender et al. 2023). Winter road maintenance and vehicle traffic, including snowmobiles, alter snowpack (Fassnacht et al. 2018), in turn affecting movement rates (Sullender et al. 2023). These effects provide a plausible mechanism for the stronger association between traffic and predator road use during winter.

Vehicle traffic plays a further role in delaying vegetation recovery by compacting soil and reducing vegetation cover (Ploughe and Fraser 2022), facilitating both human and wildlife access. Roads also experience delayed regeneration due to altered soil properties associated with road construction and vehicle traffic (Lloyd et al. 2013). Roads with vehicle traffic generally had short vegetation with low hiding cover, less forb and shrub cover, more grass cover, and permitted faster walking speed (Fig. A3).

Vehicle access can therefore sustain road function through two linked pathways. Traffic directly creates or maintains travel surfaces that influence wildlife movement and road use, particularly under winter conditions. It also maintains physical and vegetation conditions associated with efficient travel over longer periods. Roads with human access could therefore continue to function as movement corridors or hunting infrastructure for predators, potentially increasing risk to caribou. Linear disturbances can facilitate movement and increase predator encounter rates and hunting efficiency (Dickie, Serrouya, McNay et al. 2017, Dickie et al. 2020, Boucher et al. 2022).

Decommissioning measures did not consistently eliminate vehicle access

We sampled a total of 26 road sites with decommissioning comprising berms (n = 18), scarification (n = 3), planting (n = 1), and/or water crossing removal (n = 9). Because

these measures varied among sites and were represented by a limited number of targeted sites, the comparisons below are descriptive and do not estimate the effects of individual decommissioning treatments.

Roads with decommissioning had similar characteristics to roads without but tended to have taller vegetation that was less variable in height, more hiding cover and shrub cover, slightly slower walking speeds, less vehicle traffic, and to occur in older forest (Fig. A2). Nine of these roads, 35%, continued to experience vehicle traffic compared with 52% of non-primary roads without decommissioning. Although traffic occurred less frequently on roads with decommissioning, the measures represented in the sample did not consistently eliminate access.

Our cameras frequently captured traffic on roads with berms or water-crossing removals that vehicles either bypassed or gained access to through connecting roads in the network. Roads that could no longer be accessed by truck often remained accessible to all-terrain vehicles during the snow-off season and snowmobiles during the snow-on season. Roads that were scarified appeared to restrict vehicle access during the snow-off season, but vegetation remained sparse and short, even when areas were indicated as having been seeded or planted.

These observations indicate that modifying an individual road segment or installing a single barrier does not necessarily remove access. The effectiveness of a site-level measure depends on whether users can circumvent it, enter through connecting roads, or use vehicle types that remain capable of travelling on the road.

Taken together, the wildlife, road condition, and decommissioning results show that vehicle access can maintain roads as movement corridors and delay functional restoration. Traffic increased road use by wolves across seasons and by lynx during snow-on, was associated with shorter vegetation, lower hiding and shrub cover, greater graminoid cover, and faster travel conditions, and persisted on more than one-third of sampled roads with decommissioning measures. Species responses to traffic varied, but

the combined evidence shows that continued access can preserve the physical and ecological conditions through which roads remain relevant to caribou conservation.

Restoration implications

Aligned with recommendations from other studies, our findings emphasize the importance of restricting human and wildlife movement combined with restoring vegetation structure and composition (Ray 2014, Bentham and Coupal 2015, Tattersall et al. 2023). A road with continuing motorized access should remain classified as functionally active for restoration assessment purposes. Delayed revegetation on roads allows continued vehicle access, making active decommissioning imperative (Lee and Boutin 2006).

Restricting vehicle access requires road closures with access control through physical decommissioning and winter access restrictions that can be enforced. Decommissioning strategies to effectively restrict access will need to consider the broader road network and movement of various types of vehicles and species of interest across both snow-on and snow-off seasons. Effective access management should therefore include physical measures that resist circumvention, assessment of alternative entry through connected roads, consideration of trucks, all-terrain vehicles, and snowmobiles, and monitoring and enforcement after treatment.

The vehicle-traffic measure used in this study was relatively coarse, and cameras were positioned to record wildlife rather than provide precise estimates of traffic volume. The results support associations between vehicle access, wildlife use, and road condition, while the descriptive decommissioning comparison does not establish the causal effectiveness of particular treatment types.

Eliminating motorized access and reducing wildlife use are important signals that road function is diminishing. Interpreting low wildlife use as evidence of functional recovery also requires consideration of the surrounding habitat, human disturbance, and broader road-network context.

Similar road and forest use by focal mammals requires ecological interpretation

Wildlife use reflected disturbance beyond the sampled road

Several species avoided forms of human disturbance other than vehicle traffic. In one or both seasons, use intensity for wolves, lynx, and moose was higher on roads farther from primary roads (Tables A4, A5, and A7). Bears used roads more when they were farther from mines (Table A6). Hare exhibited a similar trend during the snow-off season, with effects that were nearly statistically significant (Table A8).

Use intensity decreased for wolves and lynx closer to primary roads. Predicted use intensity on non-primary roads and at forest reference sites also converged at low levels closer to primary roads (Fig. 4). This pattern shows that broader human activity can produce road–forest convergence by suppressing wildlife use. Wildlife use therefore reflected disturbance extending beyond the condition of the sampled road.

Similar road and forest use can arise through different mechanisms

Complex conditions influencing road-use intensity create challenges for identifying indicators and thresholds for functional restoration. Low use intensity by caribou predators and their prey can arise from poor habitat quality, avoidance or displacement associated with human activity or disturbance, seasonal movement conditions, or true functional recovery. Interpreting use intensity therefore requires careful consideration of the broader context in which it occurs. These context-dependent responses show why site-level patterns must be interpreted across broader disturbance settings and spatial scales (Dickie, Love et al. 2023; Barnas et al. 2024; Tjaden-McClement et al. 2025).

Avoidance of primary roads may redistribute wildlife use to other parts of the road network or surrounding habitat. Low predator use at an individual camera site provides incomplete evidence of restored function or reduced risk for caribou.

Road-use intensity for several species was also weakly associated with that of other species. Bears and hare were abundant across the study area and were the most frequently detected species, which likely contributed to small but statistically significant

associations with wolf, moose, lynx, and each other (Tables A4–A8). These relationships tended to run counter to the risk-avoidance and resource-availability hypotheses, suggesting that they could reflect species prevalence rather than direct ecological interactions. Co-occurrence or correlated detections alone do not demonstrate ecological interactions (Blanchet et al. 2020).

Restoration implications

Functional monitoring should distinguish diminishing road function from other causes of low wildlife use. Monitoring should evaluate the treated road and appropriate forest reference sites, connected roads and alternative access routes, surrounding habitat suitability, human activity and other disturbance, relevant seasons, and changes in use through time.

Criteria and thresholds should be applied as a set and interpreted against the range of natural variation in suitable reference conditions (McKellar et al. 2026). A low use estimate from a single site, species, season, or indicator may reflect functional restoration, avoidance of nearby human activity, poor surrounding habitat, or other ecological conditions. The study supports a contextual, multi-indicator assessment. It does not establish how much road–forest convergence is sufficient, which combination of indicators should be decisive, or whether low use at a site reflects redistribution of wildlife use or risk elsewhere.

Season and landscape position are therefore especially important for interpreting the significance and priority of restoration.

Season and landscape position shape restoration significance and priority

Predator road use was greatest during snow-off

The snow-off season overlaps with calving, post-calving, and summer movement periods, when calf survival can strongly influence caribou population trajectories (Gaillard et al.

2000). Federal regulations define caribou critical habitat based on known relationships between disturbance and recruitment (ECCC 2020).

Although vehicle traffic facilitated predator use more during the snow-on season, road-use intensity by predators was greatest during the snow-off season. Wolves and lynx were most active during the snow-off season. Bears also prey on calves and can be a leading cause of calf mortality (Dussault et al. 2012, Pinard et al. 2012, Leclerc et al. 2014). Increased bear use of roads could elevate calf-predation risk even where wolf detections are ambiguous, further suggesting that road restoration focused on wolves could be insufficient.

Road–forest differences were also strongest and most consistent across the full focal mammal community during snow-off (Tables A9–A13). Predator road use was therefore greatest during a period when the potential consequences for caribou recruitment may be particularly important.

These results support monitoring during snow-off months of the year, when predator activity is high and calves are vulnerable. Winter monitoring remains necessary because vehicle traffic and compacted travel surfaces can facilitate predator movement during snow-on. The study measured seasonal wildlife use of roads rather than caribou mortality or recruitment, so the results do not establish which season produces the greatest demographic effect on caribou.

Caribou and wolverine detections provide landscape context

Caribou were observed during the snow-off season on roads with and without vehicle traffic, but often near the edge of road networks (Fig. 5). We did not observe caribou at any camera sites located in the forest. We detected caribou (n = 181) on seven cameras set on roads in the northern half of the study area, most frequently around Trout Lake. Most caribou detections (n = 130) occurred at a single camera site north of Trout Lake on a road with high lichen cover and no vehicle traffic. We observed caribou at one camera site located farther from Trout Lake, near the western edge of the study area and towards Woodland Caribou Provincial Park.

Observations of wolverines (n = 185) were more widespread, spanning 26 camera sites across the study, with the fewest detections occurring in the southeastern portion of the

study area (Fig. 5). Wolverines were most consistently observed north of Trout Lake across years, in the same general area where most caribou were detected. Wolverine and caribou were both detected at one camera site in this area. We detected wolverines at camera sites on roads with and without vehicle traffic and at forest sites.

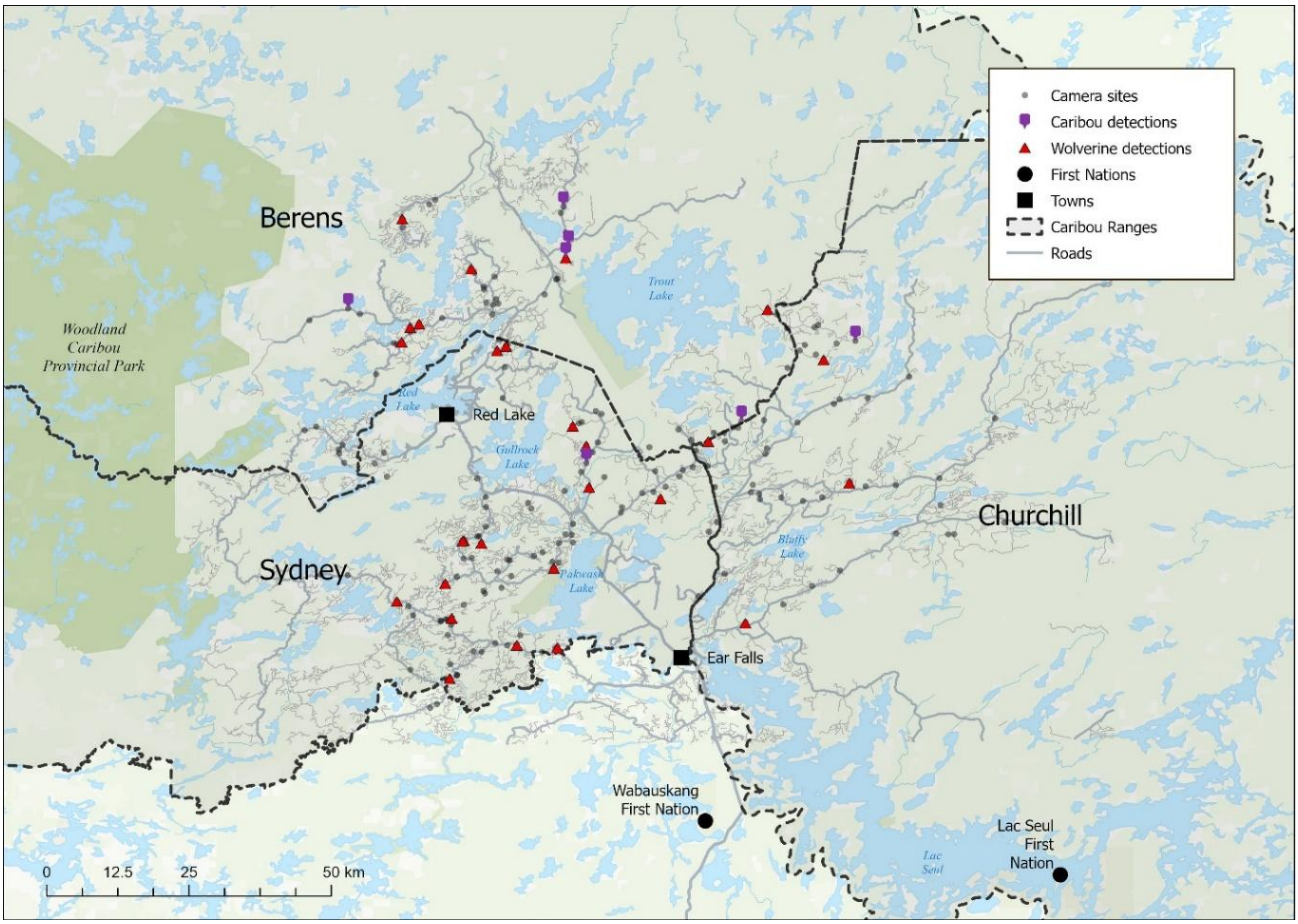

Figure 5. Caribou and wolverine detection locations during the camera-trapping survey.

Camera detections provide context rather than a direct measure of caribou response

Investigating direct caribou responses to roads with camera-trap surveys is challenging because caribou typically occur at low densities over large areas and are known to avoid roads (Leblond et al. 2012). Further understanding of how caribou themselves respond to roads would therefore be better achieved through other approaches, such as GPS-collaring programs.

As expected, we detected caribou infrequently during our study, and only in the northern portion of the study area. This spatial concentration is consistent with local reports that caribou observations have become limited to the north while deer observations have increased in the south and parallels the documented northward recession of caribou ranges in Ontario. These ranges historically extended to the north shores and islands of Lake Superior and have retracted by nearly 50% in association with human development (Racey and Armstrong 2000, Schaefer 2003). The low number and spatial concentration of detections, however, prevent stronger conclusions about current caribou distribution, habitat quality, or responses to roads within the study area.

Roads that penetrate relatively remote and intact caribou habitat may increase predator access, encounter rates, and hunting efficiency (Dickie, Serrouya, McNay et al. 2017; Dickie et al. 2020; Boucher et al. 2022). The concentration of caribou detections in the northern portion of the study area therefore provides relevant spatial context for interpreting the road-restoration results. The camera data do not identify which roads create the greatest risk to caribou or where restoration would produce the greatest reduction in mortality or population-level benefit.

Restoration implications

Restoration monitoring should include the snow-off season, when predator road use is greatest and calves are vulnerable, as well as snow-on monitoring to assess winter vehicle access and predator movement. Monitoring locations should represent the range of landscape settings in which restoration is applied, including proximity to occupied or high-quality caribou habitat and variation in road-network density, connectivity, remoteness, and surrounding disturbance.

Restoration prioritization should consider proximity to occupied or high-quality caribou habitat, whether roads penetrate relatively intact and remote areas, the density and connectivity of the surrounding road network, continuing development pressure, the feasibility of eliminating access, and the likelihood that restoration will reduce predator access or otherwise alter wildlife use. Avoiding new road access into intact or high-quality caribou habitat provides greater certainty than relying on future restoration to reverse road effects, and the possibility of future restoration should not be used to justify new road development in caribou habitat.

Together, seasonal monitoring, landscape prioritization, and prevention provide the broader context needed to apply the site-level access, road-condition, and focal-mammal-use indicators developed in the preceding sections.

A proposed framework for assessing functional restoration

The current study identifies factors influencing road use by boreal mammals relevant to caribou conservation and compares use on non-primary roads with use at forest reference sites. Together, the findings support a proposed assessment framework comprising four linked components. The framework organizes the conditions and evidence that should be considered when evaluating functional restoration. It identifies candidate indicators and directions of change. Validated thresholds, decision rules, and a definitive determination of when a road is functionally restored remain to be developed.

Functional restoration from a caribou perspective requires reducing the ecological advantages created by a road and assessing whether those changes translate into wildlife use approaching appropriate forest reference conditions. The four components should be considered together, since each addresses a different aspect of continued road function.

Component 1. Effective control of year-round motorized access

Persistent motorized access was associated with both greater use by some focal mammals and road conditions that facilitate movement. Wolves used roads with vehicle traffic more in both seasons, and lynx used roads with traffic more during the snow-on season. Roads with traffic also tended to have shorter vegetation, lower hiding and shrub cover, greater graminoid cover, and faster walking conditions. Continued traffic may therefore influence wildlife use directly while slowing the development of vegetation and physical conditions less conducive to movement. Effective control of access should be treated as a core component of functional restoration assessment.

Delayed revegetation on roads allows continued vehicle access, increasing the importance of active decommissioning (Lee and Boutin 2006).

Active decommissioning was uncommon across the study area and did not consistently eliminate access at the sampled sites. Cameras recorded traffic on roads with berms or water-crossing removals that vehicles either bypassed or reached through connecting roads. Roads that could no longer be accessed by trucks often remained accessible to all-terrain vehicles during the snow-off season and snowmobiles during the snow-on season. Because the treatments were not experimentally compared, these observations demonstrate persistent access under the sampled conditions but do not establish the relative effectiveness of individual decommissioning measures.

Assessing access control will require monitoring during both snow-on and snow-off periods, accounting for the different types of vehicles capable of using the road and for access through connecting roads or around physical barriers. Repeated monitoring may also be needed to determine whether access controls remain effective over time.

Evidence of continuing or recurrent access should be treated as an indication that road function may persist and should trigger further assessment before a road is considered functionally restored. More precise monitoring of vehicle activity will be needed to develop operational criteria for effective year-round access control.

Component 2. Reduction of movement, visibility, and vegetation-mediated advantages

Aligned with previous recommendations, our findings emphasize the importance of restricting human and wildlife movement while restoring vegetation structure and composition (Ray 2014, Bentham and Coupal 2015, Tattersall et al. 2023). Ease of movement was the most consistently supported driver of road use, although the road conditions associated with use varied among species and seasons.

Restoration treatments should reduce the functions that continue to distinguish roads from forest by obstructing physical travel, shortening sightlines, reducing graminoid dominance, promoting woody regeneration and structural complexity, and breaking up the continuity of the open corridor.

Candidate indicators include walking speed and other measures of travel efficiency, vegetation height and structural variability, hiding cover and sightlines, graminoid and woody vegetation cover, and the continuity of open, readily travelled sections of road. No single vegetation characteristic explained road use across the focal mammal community. Vegetation height alone therefore provides an insufficient basis for assessing functional restoration. Several physical and vegetation indicators should be considered together to determine whether the road continues to provide movement, visibility, forage, or cover advantages relative to surrounding forest.

These indicators describe road condition and its recovery trajectory. Wildlife use relative to forest reference conditions provides evidence of whether changes in road condition have translated into a functional outcome.

Component 3. Use by the focal mammal community relative to forest reference conditions

Mammal communities affect boreal caribou directly and indirectly through predator-prey and intraguild interactions influenced by industrial disturbance (Curveira-Santos et al. 2024). Wolves are the primary predator of adult caribou in Ontario, while bears and other predators are important sources of calf mortality. Moose and other prey can influence caribou risk through apparent competition and broader community pathways.

All five focal mammals used non-primary roads more than forest reference sites during at least part of the year. Road effects on caribou should therefore be understood as community-mediated. Responses by wolves alone provide an incomplete basis for assessing whether the ecological functions relevant to caribou have been restored.

Assessment should examine multiple focal species, or a defensible subset representing the relevant ecological pathways, and compare their use of restored roads with suitable forest reference conditions during both snow-on and snow-off periods. Reference ranges will need to account for natural variation among forest sites and through time.

The intended direction of change is for use on restored roads to approach the range observed at appropriate forest reference sites. This does not imply that use must be identical. Operational application will require reference ranges that account for natural

variation and specify how much similarity provides sufficient evidence of functional restoration.

The present study establishes the relevance of road-to-forest comparisons but does not determine how similar road and forest use must become, which focal species should receive the greatest weight, or which combination of species responses should be decisive.

Component 4. Interpretation within ecological, seasonal, and landscape context

Similar use by focal mammals on roads and at forest reference sites can arise through different mechanisms. It may reflect diminishing road function, poor surrounding habitat, avoidance of human activity, seasonal movement conditions, or potentially the redistribution of use elsewhere in the road network.

Several study results demonstrate the importance of this context. Wolves and lynx used sampled roads less near primary roads, and bears used roads less near active mines. Road use also varied with forest age, vegetation conditions, resource availability, and season. Low use by focal mammals at a particular road therefore provides incomplete evidence of functional restoration when considered in isolation.

Interpretation should account for nearby primary roads, mines and other human disturbance, surrounding habitat condition, connected roads and alternative access routes, seasonal conditions, and the road's position within the wider road network and caribou habitat. Changes in road condition and wildlife use should also be evaluated through time.

Monitoring should include both snow-off and snow-on periods. Road use by wolves and lynx was greatest during snow-off, and bears were also active during this period. Snow-on monitoring remains necessary to assess winter vehicle access, packed travel surfaces, snow conditions, and their influence on predator movement.

Caribou detections were concentrated in the northern portion of the study area, but their small number and spatial concentration do not identify which roads create the greatest

risk or where restoration would produce the greatest caribou benefit. Restoration prioritization requires independent information on caribou distribution and habitat, together with road-network configuration, surrounding disturbance, predator access, and the feasibility of controlling motorized access.

Low or similar use at a sampled road should support a functional-restoration determination only after these alternative explanations have been considered. The possibility that wildlife use or caribou risk has shifted elsewhere in the road network remains an uncertainty requiring further investigation.

Taken together, the four components provide a structured basis for assessing whether road function is diminishing. They identify relevant evidence and directions of change, but do not yet establish validated thresholds, decision rules, or a definitive determination of when a road is functionally restored.

Avoiding new access and road function in important caribou habitat provides greater certainty than relying on future restoration to reverse ecological effects. The possibility of future restoration should not be used to justify new road development in caribou habitat.

Study limitations and remaining uncertainties

This study was observational and sampled roads across existing gradients of regeneration, access, and physical condition. Active decommissioning was uncommon in the study area, and the sampled measures varied among sites. The results therefore identify conditions associated with wildlife use and continued road function, but do not establish the causal effectiveness of individual treatments or allow them to be ranked.

Camera detections provide an index of wildlife use at sampled locations rather than direct measures of abundance, movement pathways, predator-prey encounters, or demographic effects. Vehicle activity was also measured relatively coarsely, and the measured road, habitat, and disturbance variables explained only part of the variation in wildlife use. Uneven sampling of regeneration stages among years also limited the ability to separate road recovery from year-specific conditions, including potential effects of fire.

The implications for caribou remain indirect. Use of roads by the focal mammals indicates whether roads retain ecological functions relevant to caribou conservation, but the study did not measure changes in caribou survival, recruitment, or population persistence. The proposed framework identifies components and candidate indicators for assessment, while appropriate reference ranges, thresholds, and decision rules will require further testing across road conditions, restoration treatments, seasons, and landscapes, and ultimately against direct measures of caribou response.

Conclusion

This study provides valuable insights into how regenerating forestry roads continue to function differently from surrounding forest in ways relevant to boreal caribou conservation. All five focal mammals used non-primary roads more than forest reference sites during at least part of the year, with the clearest and most consistent differences occurring during snow-off. Ease of movement emerged as the most consistent mechanism maintaining road use, while vegetation structure, visibility, forage and cover conditions, motorized access, and landscape context shaped species- and season-specific responses.

The findings show that functional restoration should not be assessed from vegetation recovery alone. Assessment must consider the broader mammal community through which roads may affect caribou, together with evidence that the movement, visibility, and vegetation-mediated advantages created by the road are diminishing. The proposed framework brings together four linked components: effective control of year-round motorized access; reduction of the advantages that support continued road use; use by focal mammals relative to appropriate forest reference conditions; and interpretation within the relevant ecological, seasonal, and landscape context.

Together, these components provide a structured basis for assessing whether road function is diminishing. They identify relevant evidence and directions of change, but do not yet establish validated reference ranges, thresholds, decision rules, or a definitive determination of when a road is functionally restored. Further work is needed to test and refine these elements across road conditions, restoration treatments, seasons, and landscapes, and ultimately against direct measures of caribou response.

Avoiding new access and road function in important caribou habitat provides greater certainty than relying on future restoration to reverse ecological effects. The possibility of future restoration should not be used to justify new road development in caribou habitat.

References

Alexander, S.M., Water, N.M., and Paquet, P.C. 2005. Traffic volume and highway permeability for a mammalian community in the Canadian Rocky Mountains. Can. Geogr. 4: 322-331. https://doi.org/10.1111/j.0008-3658.2005.00099.x

Bard, S.M., and Cain III, J.W. 2020. Investigation of bed and den site selection by American black bears (Ursus americanus) in a landscape impacted by forest restoration treatments and wildfires. For. Ecol. Manag. 460: 117904. https://doi.org/10.1016/j.foreco.2020.117904

Barnas, A.F., Ladle, A., Burgar, J.M., Burton, A.C., Boyce, M.S., et al. 2024. How landscape traits affect boreal mammal responses to anthropogenic disturbance. Sci. Total Environ. 915: 169285. https://doi.org/10.1016/j.scitotenv.2023.169285

Bartoń, K. 2026. MuMIn: Multi-model inference. R package version 1.48.19, https://CRAN.R-project.org/package=MuMIn.

Beaupré, C., Joly, K., Cameron, M.D., Couriot, O., Fagan, W.F., and Gurarie, E. 2026. Winter survival shaped by forage abundance and snow depth for a long-distance migratory ungulate. Polar Biol. 49:2. https://doi.org/10.1007/s00300-025-03439-w

Benítez-López, A., Alkemade, R., and Verweij, P.A. 2010. The impacts of roads and other infrastructure on mammal and bird populations: A meta-analysis. Biol. Conserv. 143: 1307-1316. https://doi.org/10.1016/j.biocon.2010.02.009

Benoit-Pépin, A., Feldman, M.J., Imbeau, L., and Valeria, O. 2024. Use of linear features by mammal predators and prey in managed boreal forests. For. Ecol. Manag. 561: 121911. https://doi.org/10.1016/j.foreco.2024.121911

Bentham, P., and Coupal, B. 2015. Habitat restoration as a key conservation lever for woodland caribou: A review of restoration programs and key learnings from Alberta. Rangifer 35: 123-148. https://doi.org/10.7557/2.35.2.3646

Blanchet, F.G., Cazelles, C., and Gravel, D. 2020. Co-occurrence is not evidence of ecological interactions. Ecol. Lett. 23: 1050-1063. https://doi.org/10.1111/ele.13525

Bois, G., Imbeau, L., and Mazerolle, M.J. 2012. Recovery time of snowshoe hare habitat after commercial thinning in boreal Quebec. Can. . For. Res. 42: 123-133. https://doi.org/10.1139/x11-170

Boucher, N.P., Anderson, M., Ladle, A., Procter, C., Marshall, S., et al. Cumulative effects of widespread landscape change alter predator-prey dynamics. Sci. Rep. 12: 11692. https://doi.org/10.1038/s41598-022-15001-3

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., et al. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R. J. 9: 378-400. https://doi.org/10.32614/RJ-2017-066.

Crête, M., and Larivière, S. 2003. Estiating the costs of locomotion in snow for coyotes. Can. J. Zool. 81: 1808-1814. https://doi.org/10.1139/z03-182

Crins, William J., Paul A. Gray, Peter W.C. Uhlig, and Monique C. Wester. 2009. The Ecosystems of Ontario, Part I: Ecozones and Ecoregions. Ontario Ministry of Natural Resources, Peterborough Ontario, Inventory, Monitoring and Assessment, SIB TER IMA TR- 01, 71pp.

Cunningham, S.C., Ballard, W.B., Monroe, L.M., Rabe, M.T., and Bristow, K.D. 2003. Black bear habitat use in burned and unburned areas, central Arizona. Wildl. Soc. Bull. 31: 786-792. https://www.jstor.org/stable/i292266

Curveira-Santos, G., Marion, S., Sutherland, C., Beirne, C., Herdman, E.J., et al. 2024. Disturbance-mediated changes to boreal mammal spatial networks in industrializing landscapes. Ecol. Appl. 34: e3004. https://doi.org/10.1002/eap.3004

Dawe, D.A., Parisien, M.-A., Boulanger, Y., Boucher, J., Beauchemin, A., and Arseneault, D. 2021. Short- and long-term wildfire threat when adapting infrastructure for wildlife conservation in the boreal forest. Ecol. Appl. 32: e2606. https://doi.org/10.1002/eap.2606

DeMars, C.A., and Boutin, S., 2017. Nowhere to hide: Effects of linear features on predator-prey dynamics in a large mammal system. J. Anim. Ecol. 87: 274-284. https://doi.org/10.1111/1365-2656.12760

DeMars, C.A., Johnson, C.J., Dickie, M., Habib, T.J., Cody, M., et al. 2023. Incorporating mechanism into conservation actions in an age of multiple and emerging threats: The case of boreal caribou. Ecosphere 14: e4627. https://doi.org/10.1002/ecs2.4627

Dickie, M., Love, N., Steenweg, R., Lamb, C.T., Polfus, J., et al. 2023. In search of evidence-based management targets: A synthesis of the effects of linear features on woodland caribou. Ecol. Indic. 154: 110559. https://doi.org/10.1016/j.ecolind.2023.110559

Dickie, M., McNay, S.R., Sutherland, G.D., Cody, M., and Avgar, T. 2020. Corridors or risk? Movement along, and use of, linear features varies predictably among large mammal predator and prey species. J. Anim. Ecol. 89: 623-634. https://doi.org/10.1111/1365-2656.13130

Dickie, M., McNay, R.S., Sutherland, G.D., Sherman, G.G., and Cody, M. 2021. Multiple lines of evidence for predator and prey responses to caribou habitat restoration. Biol. Conserv. 256: 109032. https://doi.org/10.1016/j.biocon.2021.109032

Dickie, M., Serrouya, R., McNay, R.S., and Boutin, S. 2017a. Faster and farther: Wolf movement on linear features and implications for hunting behaviour. J. Appl. Ecol. 54: 253-263. https://doi.org/10.1111/1365-2664.12732

Dickie, M., Serrouya, R., DeMars, C., Cranston, J., and Boutin, S. 2017. Evaluating functional recovery of habitat for threatened woodland caribou. Ecosphere 8: e01936. https://doi.org/10.1002/ecs2.1936

Dickie, M., Sherman, G.G., Sutherland, G.D., McNay, R.S., and Cody, M. 2023. Evaluating the impact of caribou habitat restoration on predator and prey movement. Conserv. Biol. 37: e14004. https://doi.org/10.1111/cobi.14004

Droghini, A., and Boutin, S. 2018. The calm during the storm: Snowfall events decrease the movement rates of grey wolves (Canis lupus). PLOS ONE 13: e0205742. https://doi.org/10.1371/journal.pone.0205742

Dupee, V., V. Dinel, L. Landriault, J. Zierle, N. Dawson, L.T. Stinson and DeWitt, P.D. 2021. Ontario Wildlife Monitoring Network (OWMN) camera trap protocol for monitoring medium and large mammals. Ontario Ministry of Natural Resources and Forestry, Science and Research Branch, Peterborough, ON. Science and Research Technical Manual.

Dussault, C., Pinard, V., Ouellet J.-P., Courtois R., and Fortin, D. 2012. Avoidance of roads and selection for recent cutovers by threatened caribou: fitness-rewarding or maladaptive behaviour? Proc. Roy. Soc. B: Biol. Sci. 279(1746): 4481.

Duquette, J.F., Belant, J.L., Wilton, C.M., Fowler, N., Waller, B.W., et al. 2017. Black bear (Ursus americanus) functional resource selection relative to intraspecific competition and human risk. Can. J. Zool. 95: 203-212. https://doi.org/10.1139/cjz-2016-0031

Edwards, J. 1983. Diet shifts in moose due to predator avoidance. Oecologia 60: 185-189. https://www.jstor.org/stable/4217156

Environment and Climate Change Canada (ECCC). 2020. Amended Recovery Strategy for the Woodland Caribou (Rangifer tarandus caribou), Boreal Population, in Canada. Species at Risk Act Recovery Strategy Series. Environment and Climate Change Canada, Ottawa. xiii + 143pp.

Environment and Climate Change Canada (ECCC) & Ministry of the Environment, Conservation and Parks (MECP). (2022). Agreement for the Conservation of Caribou, Boreal Population in Ontario. Government of Canada and Government of Ontario.

Environment and Climate Change Canada (ECCC). 2024. Scientific assessment of federal and provincial frameworks for the conservation of boreal caribou in Ontario: science assessment report. Government of Canada Publications. https://publications.gc.ca/site/eng/9.936495/publication.html

Fancy, S.G., and White, R.G. 1987. Energy expenditures for locomotion by barren-ground caribou. Can. J. Zool. 65:122-128. https://doi.org/10.1139/z87-018

Fassnacht, S.R., Heath, J.T., Venable, N.B., and Elder, K.J. 2018. Snowmobile impacts on snowpack physical and mechanical properties. Cryosphere 12: 1121-1135. https://doi.org/10.5194/tc-12-1121-2018

Finnegan, L., Pigeon, K.E., Cranston, J., Hebblewhite, M., Musiani, M., Neufeld, L., Schmiegelow, F., Duval, J., Stenhouse, G.B., Festa-Bianchet, M., 2018. Natural regeneration on seismic lines influences movement behaviour of wolves and grizzly bears. PLOS ONE 13: e0195480. https://doi.org/10.1371/journal.pone.0195480

Frenette, J., Pelletier, F., and St-Laurent, M.-H. 2020. Linking habitat, predators and alternative prey to explain recruitment variations of an endangered caribou population. GECCO 22:e00920. https://doi.org/10.1016/j.gecco.2020.e00920

Fryxell, J.M., Avgar, T., Liu, B., Baker, J.A., Rodgers, A.R., et al. 2020. Anthropogenic disturbance and population viability of woodland caribou in Ontario. J. Wild. Manag. 84: 636-650. https://doi.org/10.1002/jwmg.21829

Gable, T.D., Johnson-Bice, S.M., Homkes, A.T., and Bump, J.K. 2023. Video observations of wolves hunting ungulates on linear features. Food Webs 36: e00297. https://doi.org/10.1016/j.fooweb.2023.e00297

Gaillard, J.-M., Festa-Bianchet M., Delorme D., and Jorgenson J. 2000. Body mass and individual fitness in female ungulates: bigger is not always better. Proc. Roy. Soc. Lon. B: Biol. Sci. 267(1442): 471-477.

Greenberg, S., Godin, T., and Whittington, J. 2019. Design patterns for wildlife-related camera trap image analysis. Ecology and Evolution, 9:13706-13730. https://doi.org/10.1002/ece3.5767

Hamel, S., Killengreen, S.T., Henden, J.-A., Eide, N.E., Roed-Eriksen, L., et al. 2013. Towards good practice guidance in using camera-traps in ecology: Influence of sampling design on validity of ecological inferences. Methods Ecol. Evol. 4:105-113. https://doi.org/10.1111/j.2041-210x.2012.00262.x

Hardin, J.W., and Hilbe, J.M. 2007. Generalized linear models and extensions. A Stata Press Publication, StatCorp LP, Texas.

Hartig, F. 2026. DHARMa: Residual diagnostics for hierarchical (multi-Level / mixed) regression models. R package version 0.5.0, https://github.com/florianhartig/dharma.

Hornseth, M.L., and Rempel, R.S. 2016. Seasonal resource selection of woodland caribou (Rangifer tarandus caribou) across a gradient of anthropogenic disturbance. Can. J. Zool. 94: 79-93. https://doi.org/10.1139/cjz-2015-0101

Huang, R.K.K., Webber, Q.M.R., Laforge, M.P., Robitaille, A.L., Bonar, M., et al. 2021. Coyote (Canis latrans) diet and spatial co-occurrence with woodland caribou (Rangifer tarandus caribou). Can. J. Zool. 99: 391-399. https://doi.org/10.1139/cjz-2020-0253

Hurvich, C.M. and C.L. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76: 297-307. https://doi.org/10.1093/biomet/76.2.297

Keim, J.L., Lele, S.R., DeWitt, P.D., Fitzpatrick, J.J., and Jenni, N.S. 2019. Estimating the intensity of use by interacting predators and prey using camera traps. J. Anim. Ecol. 88: 690-701. https://doi.org/10.1111/1365-2656.12960

Kittle, A.M., Anderson, M., Avgar, T., Baker, J.A., Brown, G.S., et al. Landscape-level wolf space use is correlated with prey abundance, ease of mobility, and the distribution of prey habitat. Ecosphere 8: e01783. https://doi.org/10.1002/ecs2.1783

Leblond, M., Dussault, C. and Ouellet, J.-P. 2012. Réponses comportementales du caribou forestier à l'élargissement d'un axe routier majeur. Le naturaliste canadien 136(2): 22-28.

Leblond, M., Dussault, C., and Ouellet, J.-P. 2013. Avoidance of roads by large herbivores and its relation to disturbance intensity. J. Zool. 289: 32-40. https://doi.org/10.1111/j.1469-7998.2012.00959.x

Leclerc, M., Dussault, C. and St-Laurent, M.-H. 2014. Behavioural strategies towards human disturbances explain individual performance in woodland caribou. Oecologia 176(1): 297-306.

Lee, P., and Boutin, S. 2006. Persistence and developmental transition of wide seismic lines in the western boreal plains of Canada. J. Environ. Manag. 78: 240-250. https://doi.org/10.1016/j.jenvman.2005.03.016

Lepard, C.C., Moll, R.J., Cepek, J.D., Lorch, P.D., Dennis, P.M., et al. 2018. The influence of the delay-period setting on camera-trap data storage, wildlife detections and occupancy models. Wildl. Res. 46: 37-53. https://doi.org/10.1071/WR17181

Litvaitis, J.A. 1990. Differential habitat use by sexes of snowshoe hares (Lepus Americanus). J. Mamm. 71: 520-523. https://doi.org/10.2307/1381790

Litvaitis, J.A., Sherburne, J.A., and Bissonette, J.A. 1985. Influence of understory characteristics on snowshoe hare habitat use and density. J. Wildl. Manag. 49: 866-873. https://www.jstor.org/stable/3801359

Lloyd, R.A., Lohse, K.A., and Ferré, T.P.A. 2013. Influence of road reclamation techniques on forest ecosystem recovery. Front. Ecol. Environ. 11: 75-81. https://doi.org/10.1890/120116

Loosen, A.E., Devineau O., Zimmermann B., Cromsigt, J.P.G.M., Pfeffer, S.E. Skarpe C., and Mathisen, K.M. 2021. Roads, forestry, and wolves interact to drive moose browsing behavior in Scandinavia. Ecosphere 12: e03358.

Lüdecke, D., Ben-Shachar, M.S., Patil, I., Waggoner, P., and Makowski, D. 2021. performance: An R package for assessment, comparison and testing of statistical models. J. Open Source Softw., 6:3139. https://doi.org/10.21105/joss.03139

Mackey, B.G., D.W. McKenney, C.A. Widdifield, R.A. Sims, K. Lawrence, and N. Szcyrek. 1994. A New Digital Elevation Model of Ontario. NODA/NFP Technical Report TR-6, Canadian Forest Service, Natural Resources Canada, Sault Ste. Marie, Ontario. 31pp.

Mackey, B.G., D.W. McKenney, Y.-Q. Yang, J.P. McMahon, and M.F. Hutchinson. 1996a. Site Regions Revisited: A Climatic Analysis of Hills' Site Regions for the Province of Ontario Using a Parametric Method. Canadian Journal of Forest Research, 26:333-354.

McGillycuddy, M., Warton, D.I., Popovic, G., Bolker, B.M. 2025. Parsimoniously fitting large multivariate random effects in glmmTMB." J. Stat. Softw, 112: 1-19. https://doi.org/10.18637/jss.v112.i01

McGreer, M.T., Mallon, E.E., Vander Vennen, L.M., Wiebe, P.A., Baker, J.A., et al. 2015. Selection for forage and avoidance of risk by woodland caribou (Rangifer tarandus caribou) at coarse and local scales. Ecosphere 6: 288. http://dx.doi.org/10.1890/ES15-00174.1

McKay, T.L., and Finnegan, L.A. 2022. Predator-prey co-occurrence in harvest blocks: Implications for caribou and forestry. Conserv. Sci. Pract.4: e12847. https://doi.org/10.1111/csp2.12847

McKenzie, H.W., Merrill, E.H., Spiteri, R.J., and Lewis, M.A. 2012. How linear features alter predator movement and the functional response. Interface Focus 2: 205-216. https://doi.org/10.1098/rsfs.2011.0086

MNRF. 2014a. Integrated Assessment Protocol for Woodland Caribou Ranges in Ontario. Species at Risk Branch, Thunder Bay, Ontario, vii + 95pp.

MNRF. 2014b. Integrated Range Assessment for Woodland Caribou and their Habitat: Berens Range 2012. Version 1.1. Species at Risk Branch, Thunder Bay, Ontario, x + 71pp.

MNRF. 2014c. Integrated Range Assessment for Woodland Caribou and their Habitat: Brightsand Range 2011. Species at Risk Branch, Thunder Bay, Ontario, xi + 74pp.

MNRF. 2014d. Integrated Range Assessment for Woodland Caribou and their Habitat: Churchill Range 2012. Species at Risk Branch, Thunder Bay, Ontario x + 71pp.

MNRF. 2014e. Integrated Range Assessment for Woodland Caribou and their Habitat in the Far North of Ontario: 2013. Species at Risk Branch, Thunder Bay, Ontario, xviii + 124pp.

MNRF. 2014f. Integrated Range Assessment for Woodland Caribou and their Habitat: Kesagami Range 2010. Species at Risk Branch, Thunder Bay, Ontario xi + 83pp.

MNRF. 2014g. Integrated Range Assessment for Woodland Caribou and their Habitat: Nipigon Range 2010. Species at Risk Branch, Thunder Bay, Ontario, xi + 78pp.

MNRF. 2014h. Integrated Range Assessment for Woodland Caribou and their Habitat: Pagwachuan Range 2011. Species at Risk Branch, Thunder Bay, Ontario, xi + 86pp.

MNRF. 2014i. Integrated Range Assessment for Woodland Caribou and their Habitat: Sydney Range 2012. Species at Risk Branch, Thunder Bay, Ontario, ix + 68pp.

Mumma, M.A., Gillingham, M.P., Johnson, C.J., and Parker, K.L. 2017. Understanding predation risk and individual variation in risk avoidance for threatened boreal caribou. Ecol. Evol. 7: 10266-10277. https://doi.org/10.1002/ece3.3563

Mumma, M.A., Gillingham, M.P., Parker, K.L., Johnson, C.J., and Watters M. 2018. Predation risk for boreal woodland caribou in human-modified landscapes: Evidence of wolf spatial responses independent of apparent competition. Biol. Cons. 228: 215-223.

Mumma, M.A., Gillingham, M.P., Johnson, C.J., and Parker, K.L. 2019. Functional responses to anthropogenic linear features in a complex predator-multi-prey system. Landscape Ecol. 34: 2575-2597. https://doi.org/10.1007/s10980-019-00905-9

Newton, E.J., Patterson, B.R., Anderson, M.L., Rodgers, A.R., Vander Vennen, L.M., and Fryxell, J.M. 2017. Compensatory selection for roads over natural linear features by wolves in northern Ontario: Implications for caribou conservation. PLOS ONE 12:e0186525. https://doi.org/10.1371/journal.pone.0186525

OMNR. March 2014. Forest Management Guide for Boreal Landscapes. Toronto: Queen's Printer for Ontario. 104 pp.

Ploughe, L.W., and Fraser, L.H. 2022. Find New RoadsTM? A Systematic review on the impacts of off-road vehicle activity on soil, vegetation and wildlife. Front. Ecol. Evol. 9: 805707. https://doi.org/10.3389/fevo.2021.805707

Peers, M.J.L., Majchrzak, Y.N., Menzies, A.K. et al. 2020. Climate change increases predation risk for a keystone species of the boreal forest. Nat. Clim. Chang. 10:1149-1153. https://doi.org/10.1038/s41558-020-00908-4

Pinard, V., Dussault, C., Ouellet, J.-P., Fortin, D., and Courtois, R. 2012. Calving rate, calf survival rate, and habitat selection of forest - dwelling caribou in a highly managed landscape. J. Wildlife Manag. 76(1): 189-199.

Polfus, J.L., Hebblewhite, M., and Heinemeyer, K. 2011. Identifying indirect habitat loss and avoidance of human infrastructure by northern mountain woodland caribou. Biol. Cons. 144: 2637-2646. https://doi.org/10.1016/j.biocon.2011.07.023

Popp, J.N., Hamr, J., Larkin, J.L., and Mallory, F.F. 2018. Black bear (Ursus americanus) and wolf (Canis spp.) summer diet composition and ungulate prey selectivity in Ontario, Canada. Mamm. Res. 63: 433-441. https://doi.org/10.1007/s13364-018-0368-y

Racey, G.D. and Armstrong T. 2000. Woodland caribou range occupancy in northwestern Ontario: past and present. Rangifer (2000): 173-184

Ray, J.C. 2014. Defining habitat restoration for boreal caribou in the context of national recovery: A discussion paper. Wildlife Conservation Society Canada, Toronto, Ontario, Canada.

Rytwinski, T., and Fahrig, L. 2015. The impacts of roads and traffic on terrestrial animal populations. In R. van der Ree, D. J. Smith, & C. Grilo (Eds.), Handbook of Road Ecology (pp. 237-246). John Wiley & Sons. https://onlinelibrary.wiley.com/doi/10.1002/9781118568170.ch28

Schaefer, J.A. 2003. Long - term range recession and the persistence of caribou in the taiga. Cons. Biol. 17(5): 1435-1439.

Serrouya, R., Dickie, M., Lamb, C., van Oort, H., Kelly, A.P., DeMars, C., McLoughlin, P.D., Larter, N.C., Hervieux, D., Ford, A.T., and Boutin, S. 2021. Trophic consequences of terrestrial eutrophication for a threatened ungulate. Proc. R. Soc. B 288: 20202811. https://doi.org/10.1098/rspb.2020.2811

Smith, K. 2025. An empirical assessment of the role of independence filters in temporal activity analyses using camera trapping data. Behav. Ecol. Sociobiol. 79: 2. https://doi.org/10.1007/s00265-024-03544-6

St-Laurent, M.-H., Cusson, M., Ferron, J., and Caron, A. 208. Use of residual forest by snowshoe hare in a clear-cut boreal landscape. Northeast. Nat. 15: 497-514. https://doi.org/10.1656/1092-6194-15.4.497

St-Pierre, F., Drapeau, P., and St-Laurent, M.-H. 2022. Stairway to heaven or highway to hell? How characteristics of forest roads shape their use by large mammals in the boreal forest. For. Ecol. Manag. 510: 120108. https://doi.org/10.1016/j.foreco.2022.120108

Sullender, B.K., Cunningham, C.X., Lundquist, J.D., and Prugh, L.R. 2023. Defining the danger zone: Critical snow properties for predator-prey interactions. Oikos 2023:e09925. https://doi.org/10.1111/oik.09925

Tattersall, E.R., Burgar, J.M., Fisher, J.T. and Burton, A.C. 2020. Mammal seismic line use varies with restoration: Applying habitat restoration to species at risk conservation in a working landscape. Biol. Cons. 241: 108295.

Tattersall, ER., Pigeon, K., MacNearney, D., and Finnegan, L. 2023. Walking the line: Investigating biophysical characteristics related to wildlife use of linear features. Ecol. Solut. Evid. 4: e12219. https://doi.org/10.1002/2688-8319.12219

Tjaden-McClement, K., Gharajehdaghipour, T., Shores, C., White, S., Steenweg, R., et al. 2025. Mixed evidence for disturbance-mediated apparent competition for declining caribou in western British Columbia, Canada. J. Wildl. Manag. 89: e70040. https://doi.org/10.1002/jwmg.70040

Tomchuck, P.A., Neufeld, B.T., Best, I.N., Superbie, C., Regan, C., and McLoughlin, P.D. 2026. GECCO 65: e04040. https://doi.org/10.1016/j.gecco.2025.e04040

van Sleeuwen, M. 2006. Natural Fire Regimes in Ontario. Ontario Ministry of Natural Resources, Queen's Printer for Ontario, Toronto, Ontario. 143pp.

Wehr, N.H., Boone, H.M., van den Bosch, M., Perez, A.Z., Wehr, K.L., et al. 2025. Interspecific carnivore competition and ungulate predation correlate with predator species richness. Ecology 106: e70136. https://doi.org/10.1002/ecy.70136

Wittmer, H.U., Sinclair, A.R.E., and McLellan, B.N. 2005. The role of predation in the decline and extirpation of woodland caribou. Oecologia 144: 257-267. https://doi.org/10.1007/s00442-005-0055-y

Zuur, A.F., Ieno, E.N., and Elphick, C.S. 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. and Evol.1: 3-14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

Appendix

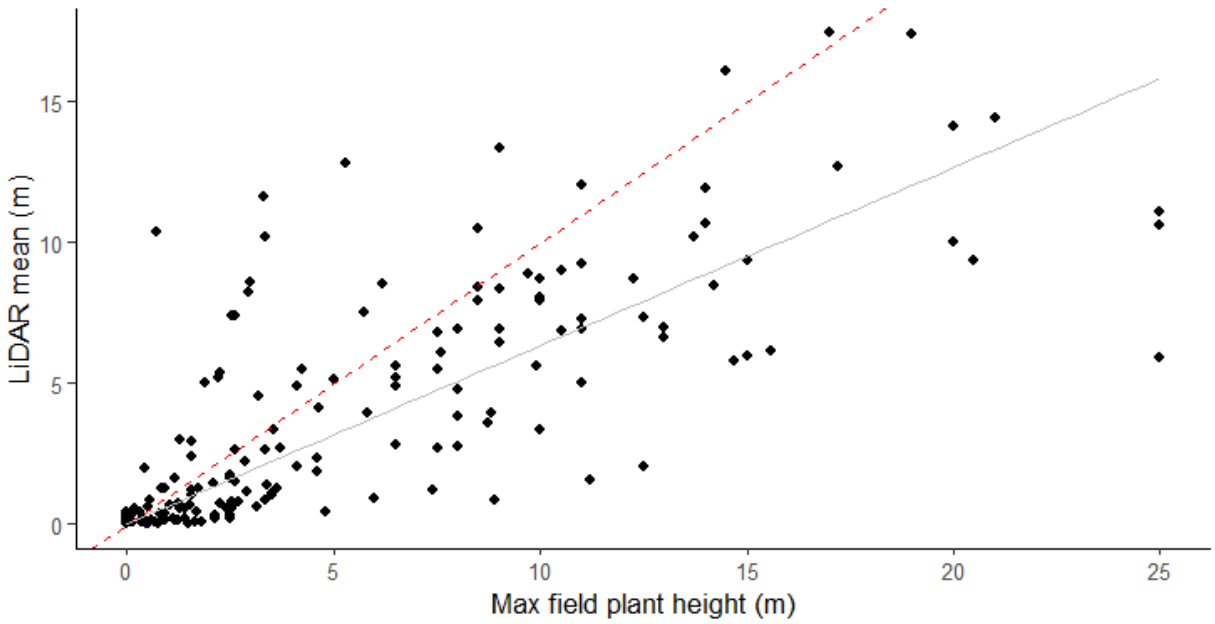

Figure A1. Relationship between maximum height measured in 100 m^2 vegetation plots in the field and mean vegetation height derived from LiDAR canopy height model. Grey line shows the linear regression through the point of origin ($y = 0.63y$, $R^2 = 0.77$); dashed red line shows a 1:1 relationship.

Table A1. Variables included in wildlife use intensity models.

variable	Definition and data source	units
forest_age	Mean forest age over 100 m National Terrestrial Ecosystem Monitoring System for Canada	years
water	Distance to nearest water source	km
mean_height	Mean vegetation height derived from LiDAR Canopy Height Model over 100m Forest Resources Inventory leaf on LiDAR	m
cv_height	Coefficient of variation of vegetation height derived from LiDAR Canopy Height Model over 100 m Forest Resources Inventory leaf on LiDAR	m
rel_speed	Walking speed in forest/walking speed on road over 50 m	-
rel_cover0.5	Percent hiding cover in forest/percent hiding cover on road at height of 0.5 m	-
rel_cover1.5	Percent hiding cover in forest/percent hiding cover on road at height of 1.5 m	-
mine	Distance to nearest active mine Principal Mineral Areas, Producing Mines, and Oil and Gas Fields (900A) - Open Government Portal	km
primary	Distance to nearest primary road Ontario Road Network (ORN) Road Net Element | Ontario GeoHub	km
human_activity	Frequency of vehicle traffic (none, < monthly, monthly, weekly, daily)	-
lichen	Percent cover of lichens in 100 m vegetation plot	%
graminoid	Percent cover of graminoids in 100 m vegetation plot	%
forb	Percent cover of forbs in 100 m vegetation plot	%
shrub	Percent cover of shrubs in 100 m vegetation plot	%
sapling	Percent cover of sapling (tree height < 5 m) in 100 m vegetation plot	%
hare	Snowshoe hare daily use intensity	detections
moose	Moose daily use intensity	detections
wolf	Wolf daily use intensity	detections
lynx	Lynx daily use intensity	detections
bear	Bear daily use intensity	detections
site_ID	Camera site unique identifier	-
nearest_primary	Nearest primary road to camera site	-

Table A2. Hypothesis-driven candidate models ranked with Akaike's Information Criterion for each species and season. All models included random intercepts for camera site (1| site_ID) site and nearest primary road (1| nearest_primary_ID). See Table A3 for season- and species-specific model formulas for individual hypotheses.

model #	hypothesis
1	null
2	res
3	move
4	risk
5	dist
6	res + move
7	res + risk
8	res + dist
9	move + risk
10	move + dist
11	risk + dist
12	res + move + risk
13	res + move + dist
14	res + risk + dist
15	move + risk + dist
16	res + move + risk + dist

Table A3. Species- and season-specific model formulas for hypothesized drivers related to resource availability (res), ease of movement (move), risk avoidance (risk), and human disturbance (dist).

species	hypothesis	formula	
		snow-off	snow-on
wolf	res	~ forest_age + water + hare + moose	~ forest_age + water + hare + moose
	move	~ mean_height + cv_height + rel_speed + rel_cover0.5	~ mean_height + cv_height + rel_speed + rel_cover0.5
	risk	~ lynx + bear	~ lynx
	dist	~ mine + primary + human_activity	~ mine + primary + human_activity
bear	res	~ forest_age + water + hare + moose + shrub	
	move	~ mean_height + cv_height + rel_speed + rel_cover0.5	
	risk	~ wolf + lynx	
	dist	~ mine + primary + human_activity	
moose	res	~ forest_age + water + graminoid + forb + shrub + sapling	~ forest_age + water + lichen + shrub + sapling
	move	~ mean_height + cv_height + rel_speed + rel_cover1.5	~ mean_height + cv_height + rel_speed + rel_cover1.5
	risk	~ wolf + lynx + bear	~ wolf + lynx
	dist	~ mine + primary + human_activity	~ mine + primary + human_activity
lynx	res	~ forest_age + water + hare + moose	~ forest_age + water + hare + moose
	move	~ mean_height + cv_height + rel_speed + rel_cover0.5	~ mean_height + cv_height + rel_speed + rel_cover0.5
	risk	~ wolf + bear	~ wolf
	dist	~ mine + primary + human_activity	~ mine + primary + human_activity
hare	res	~ forest_age + water + graminoid + forb + shrub + sapling	
	move	~ mean_height + cv_height + rel_speed + rel_cover0.5	
	risk	~ wolf + lynx + bear	
	dist	~ mine + primary + human_activity	

Table A4. Wolf road use intensity model coefficient estimates for highest-ranked models during the snow-on and snow-off seasons.

		fixed			random	
hypothesis [model]	variable	b	SE	p	variance	sd
snow-on						
	intercept	-5.84118	0.28574	<2e-16		
	mean_height	-0.5504	0.28154	0.050736		
	cv_height	-0.05301	0.11344	0.64029		
	rel_speed	0.15477	0.14528	0.286725		
	rel_cover0.5	**0.25437**	**0.09997**	**0.01094**		
	mine	-0.1942	0.13619	0.153886		
move + dist [m10]	**primary**	**0.25606**	**0.09972**	**0.010231**		
	human_activity <monthly	1.01432	0.38291	0.08074		
	human_activity monthly	**1.31745**	**0.42314**	**0.001848**		
	human_activity weekly	**1.72993**	**0.41126**	**2.59E-05**		
	human_activity daily	**1.67734**	**0.44313**	**0.000154**		
	nearest_primary				7.69E-07	0.000877
	site_ID				7.60E-01	0.875233
	intercept	-5.83597	0.28518	<2e-16		
	mean_height	-0.54759	0.2808	0.051162		
	cv_height	-0.05175	0.11306	0.647136		
	rel_speed	0.15391	0.14486	0.288043		
move + risk + dist	**rel_cover0.5**	**0.25226**	**0.09961**	**0.01133**		
[m15]	lynx	0.03456	0.03211	0.281784		
	mine	-0.19403	0.13576	0.152959		
	primary	**0.25351**	**0.0994**	**0.010761**		
	human_activity <monthly	**1.00982**	**0.3819**	**0.008188**		

	human_activity monthly	**1.31551**	**0.42212**	**0.0001831**		
	human_activity weekly	**1.71749**	**0.41035**	**2.85E-05**		
	human_activity daily	**1.67414**	**0.44218**	**0.000153**		
	nearest_primary				1.58E-07	0.000397
	site_ID				7.58E-01	0.870823
snow-off						
	intercept	-4.97882	0.2457	<2e-16		
	mean_height	-0.50493	0.32982	0.1258		
	cv_height	0.343796	0.218286	0.1153		
	rel_speed	0.389368	0.203497	0.0557		
move + risk [m9]	rel_cover0.5	0.231438	0.184648	0.2101		
	lynx	0.005583	0.027972	0.8418		
	bear	**0.04517**	**0.020907**	**0.0307**		
	nearest_primary				2.10E-01	0.4582
	site_ID				1.61E+00	1.2663
	intercept	-4.9688	0.2466	<2e-16		
	mean_height	-0.5104	0.3312	0.1233		
	cv_height	0.3457	0.2194	0.115		
move [m3]	rel_speed	0.3902	0.2044	0.0562		
	rel_cover0.5	0.2333	0.1855	0.2086		
	nearest_primary				2.12E-01	0.4608
	site_ID				1.62E+00	1.2742
	intercept	-5.334	0.329925	<2e-16		
	mean_height	-0.2882	0.365919	0.4309		
move + risk + dist	cv_height	0.271896	0.213525	0.2029		
[m15]	rel_speed	0.400836	0.209679	0.0559		
	rel_cover0.5	0.266328	0.190395	0.1619		
	lynx	0.004757	0.02804	0.8651		

bear	**0.045681**	**0.021084**	**0.0303**		
mine	0.031831	0.204108	0.8762		
primary	**0.307602**	**0.145014**	**0.0339**		
human_activity <monthly	0.653393	0.504931	0.1957		
human_activity monthly	**1.203945**	**0.552023**	**0.0292**		
human_activity weekly	0.755001	0.53702	0.1598		
human_activity daily	0.706571	0.549684	0.1986		
nearest_primary				1.55E-06	0.001245
site_ID				1.75E+00	1.321958

Table A5. Lynx road use intensity model coefficient estimates for highest-ranked models during the snow-on and snow-off seasons.

		fixed			random	
hypothesis [model]	variable	b	SE	p	variance	sd
snow-on						
res + move + dist [m13]	intercept	-5.45355	0.287293	<2e-16		
	forest_age	**-0.4525**	**0.134542**	**0.00077**		
	water	-0.10776	0.130533	0.409076		
	hare	-0.02075	0.056444	0.713105		
	moose	0.000585	0.02607	0.982093		
	mean_height	**-0.66677**	**0.2733**	**0.014699**		
	cv_height	**-0.27751**	**0.138397**	**0.044947**		
	rel_speed	0.094681	0.160089	0.554233		
	rel_cover0.5	0.212137	0.118043	0.072316		
	mine	-0.2362	0.17239	0.170636		
	primary	**0.423403**	**0.122755**	**0.000562**		
	human_activity <monthly	0.673544	0.368803	0.067806		
	human_activity monthly	0.714074	0.401145	0.075061		
	human_activity weekly	**1.198296**	**0.394674**	**0.002396**		
	human_activity daily	0.800089	0.446445	0.073112		
	nearest_primary				0.2814	0.5305
	site_ID				0.9984	0.9992
res + move + risk + dist [m16]	intercept	-5.45269	0.287225	<2e-16		
	forest_age	**-0.45298**	**0.134523**	**0.000759**		
	water	-0.1072	0.130512	0.411425		
	hare	-0.02089	0.056478	0.711487		
	moose	0.000399	0.02621	0.987942		
	mean_height	**-0.66644**	**0.273251**	**0.014731**		

	cv_height	**-0.2774**	**0.138358**	**0.044969**		
	rel_speed	0.094626	0.160075	0.554429		
	rel_cover0.5	0.211461	0.118023	0.073184		
	wolf	0.015232	0.035714	0.669755		
	mine	-0.23519	0.172332	0.172334		
	primary	**0.423287**	**0.122729**	**0.000563**		
	human_activity <monthly	0.673278	0.368728	0.067858		
	human_activity monthly	0.712857	0.401075	0.075508		
	human_activity weekly	**1.195356**	**0.394686**	**0.002457**		
	human_activity daily	0.796201	0.446516	0.074563		
	nearest_primary				0.2809	0.53
	site_ID				0.9979	0.9989
snow-off						
	intercept	-4.19987	0.225194	<2e-16		
	forest_age	-0.19982	0.13259	0.131802		
	water	0.07209	0.129779	0.578564		
	hare	0.018094	0.053666	0.735997		
	moose	**-0.09517**	**0.046363**	**0.040095**		
	mean_height	-0.07457	0.237966	0.753999		
res + move	cv_height	-0.08353	0.171148	0.625495		
+ risk + dist	rel_speed	0.222818	0.151195	0.140558		
[m16]	**rel_cover0.5**	**0.335267**	**0.151959**	**0.027363**		
	wolf	-0.00481	0.023654	0.838995		
	bear	**0.049427**	**0.017708**	**0.00525**		
	mine	0.118304	0.160502	0.46107		
	primary	**0.444274**	**0.119426**	**1.99E-04**		
	human_activity <monthly	0.222313	0.351815	0.52745		
	human_activity monthly	0.535757	0.403235	0.183965		

	human_activity weekly	0.259012	0.390587	0.507243		
	human_activity daily	0.2496	0.403479	0.536167		
	nearest_primary				1.71E-01	0.414
	site_ID				0.8415	0.9173
move + res + dist [m15]	intercept	-4.2248	0.224488	<2e-16		
	mean_height	-0.12512	0.237175	0.597821		
	cv_height	-0.12031	0.169907	0.478897		
	rel_speed	0.179385	0.147979	0.225426		
	rel_cover0.5	0.293937	0.15018	0.050319		
	wolf	-0.00385	0.023599	0.870375		
	bear	**0.04925**	**0.17717**	**0.005438**		
	mine	0.110727	0.158303	0.484264		
	primary	**0.389082**	**0.113205**	**0.000588**		
	human_activity <monthly	0.304612	0.350638	0.384991		
	human_activity monthly	0.617295	0.40236	0.124984		
	human_activity weekly	0.321148	0.391161	0.411639		
	human_activity daily	0.305407	0.403791	0.44944		
	nearest_primary				1.43E-01	0.3785
	site_ID				0.8732	0.9345

Table A6. Bear road use intensity model coefficient estimates for highest-ranked models during the snow-off season.

		fixed			random	
hypothesis [model]	variable	b	SE	p	variance	sd
snow-off						
	intercept	-2.75679	0.13349	<2e-16		
	forest_age	-0.06731	0.08388	0.42231		
	water	-0.01062	0.08792	0.90389		
	hare	**0.08383**	**0.03564**	**0.01866**		
	moose	0.0388	0.0251	0.12212		
	forb	0.13305	0.08854	0.13292		
res + move + risk + dist [m16]	**mean_height**	**-0.33338**	**0.15956**	**0.03668**		
	cv_height	0.0464	0.11183	0.67818		
	rel_speed	**0.2479**	**0.09669**	**0.01035**		
	rel_cover0.5	**0.22918**	**0.10082**	**0.02301**		
	wolf	0.03462	0.02042	0.09003		
	lynx	**0.06146**	**0.02238**	**0.00603**		
	mine	**0.20136**	**0.09572**	**0.03542**		
	primary	0.11573	0.0769	0.13233		
	human_activity <monthly	-0.07039	0.22974	0.75932		
	human_activity monthly	-0.34763	0.29587	0.24001		

	human_activity weekly	-0.44883	0.26879	9.47E-02		
	human_activity daily	**-1.21322**	**0.30356**	**6.42E-05**		
	nearest_primary				2.01E-08	0.000142
	site_ID				4.47E-01	0.668786
move + risk + dist [m15]	intercept	-2.75771	0.13521	<2e-16		
	mean_height	**-0.36134**	**0.15939**	**0.02339**		
	cv_height	0.05219	0.11206	0.6414		
	rel_speed	**0.23088**	**0.09613**	**0.01632**		
	rel_cover0.5	0.18012	0.09951	0.07029		
	wolf	0.03384	0.02049	0.09872		
	lynx	**0.06045**	**0.02243**	**0.00704**		
	mine	**0.24851**	**0.09455**	**0.00858**		
	primary	0.1077	0.0732	0.141119		
	human_activity <monthly	-0.06158	0.23164	0.79036		
	human_activity monthly	-0.33922	0.29783	0.25472		
	human_activity weekly	-0.47151	0.27167	8.26E-02		
	human_activity daily	**-1.25035**	**0.30629**	**4.46E-05**		
	nearest_primary				2.12E-08	0.000146
	site_ID				4.69E-01	0.684499

Table A7. Moose road use intensity model coefficient estimates for highest-ranked models during the snow-on and snow-off seasons.

		fixed			random	
hypothesis [model]	variable	b	SE	p	variance	sd
snow-on						
	intercept	-5.30431	0.198324	<2e-16		
	forest_age	-0.13282	0.144982	0.34914		
	water	0.004132	0.144982	0.97726		
	lichen	-0.51654	0.299205	0.08428		
	shrub	0.272887	0.161486	0.09106		
	sapling	0.257649	0.138728	0.06328		
	mean_height	**-0.81193**	**0.251097**	**0.00122**		
	cv_height	-0.07954	0.147281	0.58891		
	rel_speed	**0.424318**	**0.152787**	**0.00548**		
	rel_cover1.5	0.096382	0.13925	0.48884		
	nearest_primary				2.47E-08	0.000157
	site_ID				1.10E+00	1.049705
snow-off						
res + move + risk + dist [m16]	intercept	-4.00132	0.172745	<2e-16		
	forest_age	-0.05621	0.112074	0.61596		
	water	-0.03513	0.107216	7.43E-01		
	graminoid	**0.23906**	**0.092985**	**1.02E-02**		
	forb	-0.12976	0.131158	0.3445		
	shrub	-0.21976	0.134236	0.1016		
	sapling	0.097385	0.107275	0.36398		
	mean_height	**-0.4013**	**0.199846**	**0.04464**		

	cv_height	**-0.3229**	**0.143406**	**0.02434**		
	rel_speed	**0.285483**	**0.116693**	**0.01443**		
	rel_cover1.5	1.47E-01	1.30E-01	0.25847		
	wolf	-3.43E-03	3.29E-02	0.91715		
	lynx	**-1.01E-01**	**4.88E-02**	**0.03779**		
	bear	**5.29E-02**	**2.13E-02**	**0.01295**		
	mine	-1.04E-01	1.29E-01	0.41886		
	primary	**2.48E-01**	**9.44E-02**	**0.00866**		
	human_activity <monthly	1.67E-01	2.82E-01	0.55373		
	human_activity monthly	2.18E-01	3.61E-01	0.54564		
	human_activity weekly	-3.13E-01	3.46E-01	0.3662		
	human_activity daily	-3.33E-02	3.53E-01	0.92477		
	nearest_primary				4.78E-08	0.000219
	site_ID				5.15E-01	0.717937
move + risk + dist [m15]	intercept	-4.0744	0.180308	<2e-16		
	mean_height	**-0.46976**	**0.202388**	**0.02028**		
	cv_height	**-0.28256**	**0.140791**	**0.04475**		
	rel_speed	**0.324106**	**0.11281**	**0.00407**		
	rel_cover1.5	1.33E-01	1.23E-01	0.28		
	wolf	-2.84E-03	3.29E-02	0.9312		
	lynx	**-1.03E-01**	**4.89E-02**	**0.03581**		
	bear	**5.37E-02**	**2.13E-02**	**0.01152**		
	mine	-6.92E-02	1.23E-01	0.57473		
	primary	**2.43E-01**	**8.99E-02**	**0.00681**		
	human_activity <monthly	3.81E-01	2.88E-01	0.18691		
	human_activity monthly	4.28E-01	3.67E-01	0.24328		
	human_activity weekly	-1.78E-01	3.56E-01	0.61767		
	human_activity daily	7.88E-02	6.31E-01	0.82731		

	nearest_primary				3.19E-08	0.000179
	site_ID				6.18E-01	0.785943
res + move + risk [m12]	intercept	-3.99357	0.137487	<2e-16		
	forest_age	0.009451	0.125206	0.93983		
	water	-0.01034	0.114793	9.28E-01		
	graminoid	**0.281319**	**0.092905**	**2.46E-03**		
	forb	-0.05828	0.142073	0.68163		
	shrub	-0.15179	0.135118	0.26129		
	sapling	0.148032	0.110162	0.17902		
	mean_height	-0.46051	0.189464	0.01507		
	cv_height	-0.26792	0.14592	0.06634		
	rel_speed	**0.276359**	**0.12234**	**0.02389**		
	rel_cover1.5	1.12E-01	1.34E-01	0.40373		
	wolf	-3.78E-03	3.32E-02	0.9093		
	lynx	**-9.75E-02**	**4.88E-02**	**0.04595**		
	bear	**5.30E-02**	**2.11E-02**	**0.01207**		
	nearest_primary				8.20E-02	0.2863
	site_ID				5.07E-01	0.7123

Table A8. Hare road use intensity model coefficient estimates for highest-ranked models during the snow-off seasons.

		fixed			random	
hypothesis [model]	variable	b	SE	p	variance	sd
snow-on						
	intercept	-2.28405	0.192967	<2e-16		
	forest_age	**-0.41592**	**0.123802**	**0.000781**		
	water	-0.0889	0.115616	0.441943		
	shrub	-0.04402	0.138146	0.750012		
	sapling	-0.00344	0.118878	0.976895		
	mean_height	0.356217	0.216353	0.099668		
	cv_height	-0.13832	0.141542	0.328447		
res + move	rel_speed	-0.09963	0.134991	0.46049		
+ dist	rel_cover0.5	-0.22141	0.137791	0.108081		
[m16]	mine	0.056627	0.14006	0.685987		
	primary	0.210404	0.116936	0.071971		
	human_activity <monthly	-0.46226	0.312986	0.139697		
	human_activity monthly	-0.48588	0.344008	0.157828		
	human_activity weekly	**-0.90592**	**0.39688**	**0.022453**		
	human_activity daily	**-3.41106**	**1.081196**	**0.001606**		
	nearest_primary				0.03971	0.1993
	site_ID				1.16197	1.0779
	intercept	-2.2864	0.193213	<2e-16		
	forest_age	**-0.41766**	**0.123919**	**0.000751**		
res + move	water	-0.08925	0.115678	0.4404		
+ risk +	shrub	-0.44016	0.138222	0.750146		
dist [m16]	sapling	-0.00365	0.11893	0.975548		
	mean_height	0.355521	0.216455	0.100493		
	cv_height	-0.13893	0.141598	0.326532		

	rel_speed	-0.09974	0.135068	0.460267		
	rel_cover0.5	-0.22	0.137876	0.110535		
	wolf	0.002554	0.038621	0.947271		
	lynx	-0.01823	0.027728	0.510887		
	mine	0.056575	0.140173	0.686507		
	primary	0.211753	0.117049	0.070435		
	human_activity <monthly	-0.46236	0.313147	0.139811		
	human_activity monthly	-0.48488	0.344148	0.158859		
	human_activity weekly	**-0.90085**	**0.397179**	**0.023322**		
	human_activity daily	**-3.4112**	**1.081**	**0.001606**		
	nearest_primary				0.04033	0.2008
	site_ID				1.16286	1.0784
snow-off						
move + dist [m10]	intercept	-3.04858	0.27417	<2e-16		
	mean_height	**0.82523**	**0.29666**	**0.00541**		
	cv_height	0.0176	0.2365	0.94066		
	rel_speed	0.03565	0.17909	0.84219		
	rel_cover0.5	-0.23521	0.2213	0.28783		
	mine	0.38566	0.19823	0.05171		
	primary	0.17294	0.14906	0.24596		
	human_activity <monthly	-0.25369	0.45023	0.57312		
	human_activity monthly	0.05447	0.48636	0.91083		
	human_activity weekly	0.01132	0.48525	0.98139		
	human_activity daily	-0.56479	0.5613	0.31432		
	nearest_primary				1.81E-01	0.4254
	site_ID				1.8	1.3418
	intercept	-3.06584	0.27407	<2e-16		
	mean_height	**0.83215**	**0.29617**	**0.00496**		

move +	cv_height	0.01709	0.2361	0.94228
risk + dist	rel_speed	0.03307	0.17883	0.85329
[m15]	rel_cover0.5	-0.24749	0.22116	0.2631

	wolf	0.1875	0.0259	0.46915		
	lynx	0.0127	0.02445	0.60361		
	bear	**0.03625**	**0.01584**	**0.02209**		
	mine	0.38196	0.19807	0.05381		
	primary	0.1697	0.149	0.25474		
	human_activity <monthly	-0.25074	0.44951	0.57697		
	human_activity monthly	0.05833	0.48576	0.90441		
	human_activity weekly	0.02919	0.48477	0.95198		
	human_activity daily	-0.5364	0.56053	0.3386		
	nearest_primary				1.83E-01	0.4277
	site_ID				1.7923	0.13388
	intercept	-3.17941	0.19977	<2e-16		
	mean_height	**0.82459**	**0.28382**	**0.00367**		
	cv_height	0.02437	0.24199	0.91977		
move [m3]	rel_speed	-0.06963	0.18033	0.69939		
	rel_cover0.5	-0.36729	0.21679	0.09022		
	nearest_primary				2.02E-01	0.4494
	site_ID				1.9637	1.4013
	intercept	-3.19099	0.19919	<2e-16		
	mean_height	**0.82883**	**0.28267**	**0.00337**		
	cv_height	0.02286	0.24108	0.93446		
	rel_speed	-0.07072	0.17966	0.69386		
move +	rel_cover0.5	-0.37314	0.21617	0.08433		
risk [m9]	wolf	0.01765	0.02589	0.49545		
	lynx	0.01256	0.02435	0.60586		
	bear	**0.03693**	**0.01577**	**0.01924**		
	nearest_primary				2.01E-01	0.4485
	site_ID				1.9463	1.3951

Table A9. Wolf non-primary road and forest use intensity model coefficient estimates during the snow-on and snow-off seasons.

		fixed			random			
season	variable	b	SE	p	variance	sd	conditional R^2	marginal R^2
snow-on							0.543	0.372
	intercept	-6.4162	0.3816	<2e-16				
	primary	**0.2851**	**0.1317**	**0.0304**				
	rel_cover0.5	-0.3219	0.2093	0.1241				
	site_type forest	**-2.6129**	**1.081**	**0.0156**				
	vehicle_activity yes	**1.8183**	**0.4346**	**2.86E-05**				
	nearest_primary				1.43E-08	1.20E-04		
	site_ID				1.54E+00	1.239716		
snow-off							0.494	0.248
	intercept	-5.77738	0.33554	<2e-16				
	bear	0.0376	0.02926	0.19877				
	primary	**0.36075**	**0.14506**	**0.01289**				
	vehicle_activity yes	**1.6459**	**0.41062**	**6.12E-05**				
	site_type forest	**-1.70699**	**0.62293**	**0.00614**				
	nearest_primary				3.78E-08	0.000194		
	site_ID				1.91E+00	1.381342		

Table A10. Moose non-primary road and forest use intensity model coefficient estimates during the snow-on and snow-off seasons.

		fixed			random			
season	variable	b	SE	p	variance	sd	conditional R^2	marginal R^2
							0.412	0.155
	intercept	-5.4626	0.2746	<2e-16				
	mean_height	-0.2811	0.2324	0.2266				
snow-on	**walking_speed**	**-0.7475**	**0.3251**	**0.0215**				
	site_type forest	-0.7308	0.5471	0.1816				
	nearest_primary				2.74E-01	0.5235		
	site_ID				1.72E+00	1.3117		
							0.345	0.199
	intercept	-4.1354	0.150772	<2e-16				
	graminoid	**0.267893**	**0.102257**	**8.80E-03**				
	mean_height	0.002864	0.156163	0.98537				
	walking_speed	**-0.64208**	**0.220075**	**0.00353**				
snow-off	lynx	-1.03E-01	6.21E-02	0.09608				
	bear	**5.57E-02**	**2.43E-01**	**0.02173**				
	primary	1.88E-01	9.62E-02	0.05041				
	site_type forest	**-7.91E-01**	**3.48E-01**	**0.02285**				
	nearest_primary				2.50E-07	0.0005		
	site_ID				8.04E-01	0.896383		

Table A11. Lynx non-primary road and forest use intensity model coefficient estimates during the snow-on and snow-off seasons.

		fixed			random			
season	variable	b	SE	p	variance	sd	conditional R^2	marginal R^2
							0.495	0.303
	intercept	-5.5629	0.2785	<2e-16				
	forest_age	**-0.4363**	**0.1638**	**0.00772**				
	mean_height	**-0.7401**	**0.2469**	**0.00272**				
snow-on	**primary**	**0.3185**	**0.1419**	**0.02484**				
	vehicle_activity yes	**1.0447**	**0.3708**	**0.00484**				
	site_type forest	-0.6493	0.4974	0.19181				
	nearest_primary				0.02552	0.1597		
	site_ID				1.40241	1.1842		
							0.455	0.333
	intercept	-4.04041	0.15402	<2e-16				
	moose	-0.10079	0.06067	0.09666				
	cover_0.5	**-0.36729**	**0.12985**	**0.00467**				
snow-off	bear	0.02964	0.02396	0.21597				
	primary	**0.37297**	**0.11384**	**1.05E-03**				
	site_type forest	**-3.02586**	**0.47682**	**2.21E-10**				
	nearest_primary				8.18E-02	0.2859		
	site_ID				0.79788	0.8932		

Table A12. Hare non-primary road and forest use intensity model coefficient estimates during the snow-on and snow-off seasons.

		fixed			random			
season	variable	b	SE	p	variance	sd	conditional R^2	marginal R^2
							0.401	0.057
	intercept	-1.9661	0.1682	<2e-16				
	forest_age	**-0.2875**	**0.1057**	**0.00651**				
snow-on	site_type forest	-0.5179	0.2701	0.05515				
	vehicle_activity yes	**-0.9759**	**0.2457**	**7.12E-05**				
	nearest_primary				5.72E-08	0.000239		
	site_ID				1.333	1.154511		
							0.52	0.11
	intercept	-2.8359	0.1853	<2e-16				
	mean_height	**0.5783**	**0.1774**	**0.00111**				
snow-off	**bear**	**0.0323**	**0.0158**	**0.04098**				
	site_type forest	-1.8368	0.3857	1.91E-06				
	nearest_primary				1.11E-01	0.3331		
	site_ID				1.9507	1.3967		

Table A13. Bear non-primary road and forest use intensity model coefficient estimates during the snow-off season.

		fixed			random			
season	variable	b	SE	p	variance	sd	conditional R^2	marginal R^2
							0.268	0.16
snow-off	intercept	-2.778	0.12766	<2e-16				
	hare	0.05434	0.03284	0.098				
	mean_height	**-0.32173**	**0.10862**	**0.00306**				
	walking_speed	**-0.35356**	**0.11821**	**0.00278**				
	rel_cover0.5	-0.18617	0.09533	0.05082				
	lynx	0.03687	0.02352	0.11695				
	mine	**0.21784**	**0.07535**	**0.0384**				
	site_type forest	**-0.69802**	**0.2185**	**1.40E-03**				
	vehicle_activity yes	-0.15121	0.22309	4.98E-01				
	nearest_primary				1.58E-08	0.000126		
	site_ID				4.36E-01	0.660546		

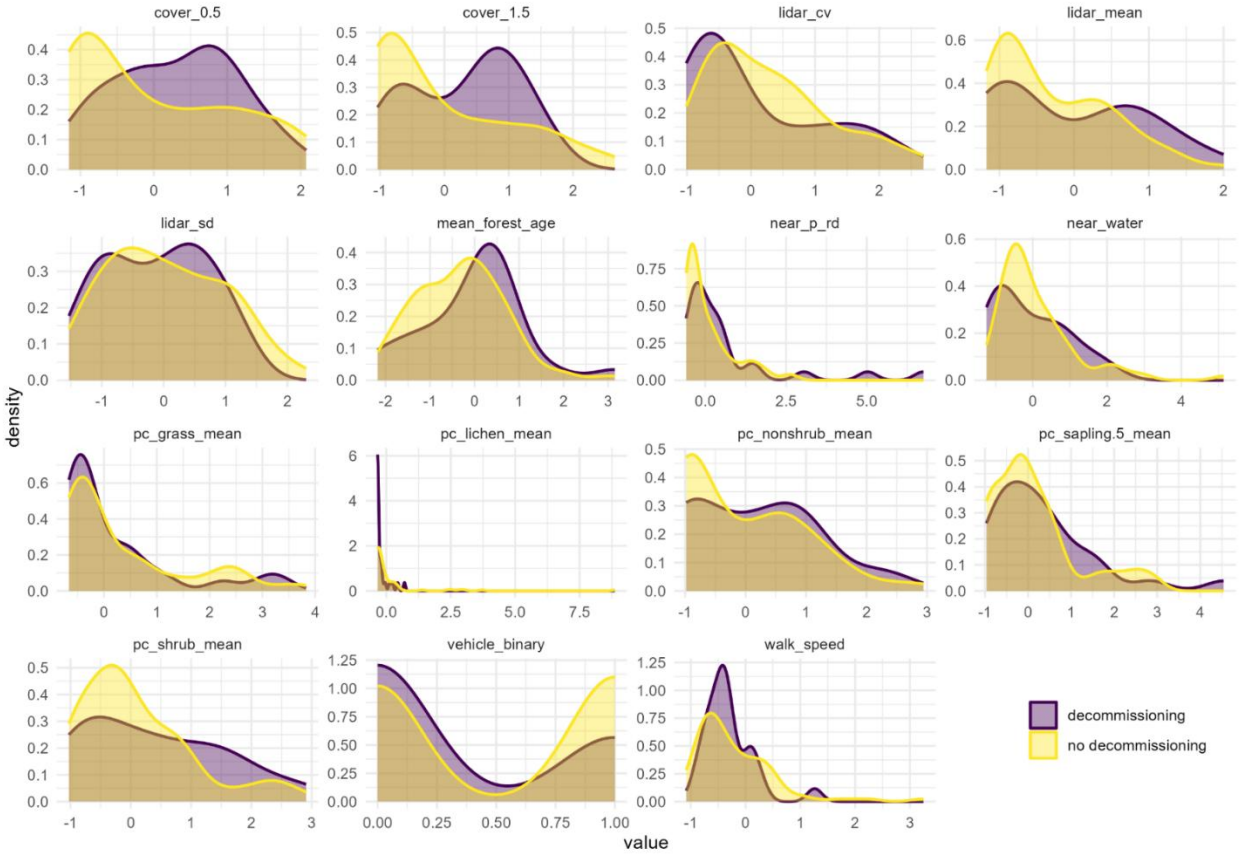

Figure A2. Distributions comparing standardized characteristics of roads with and without active decommissioning (berms, scarification, water-crossing removal, and/or seeding/planting). Panels from top left to bottom right show percent hiding cover a 0.5 m height, percent hiding cover at 1.5 m height, coefficient of variation of vegetation height over 100 m, mean vegetation height over 100 m, standard deviation of vegetation height over 100 m, mean age of surrounding forest within 100 m radius, distance to nearest primary road, distance to nearest waterbody, percent grass cover, percent lichen cover, percent forb cover, percent sapling cover, percent shrub cover, vehicle traffic presence/absence, and time to walk 50 m.

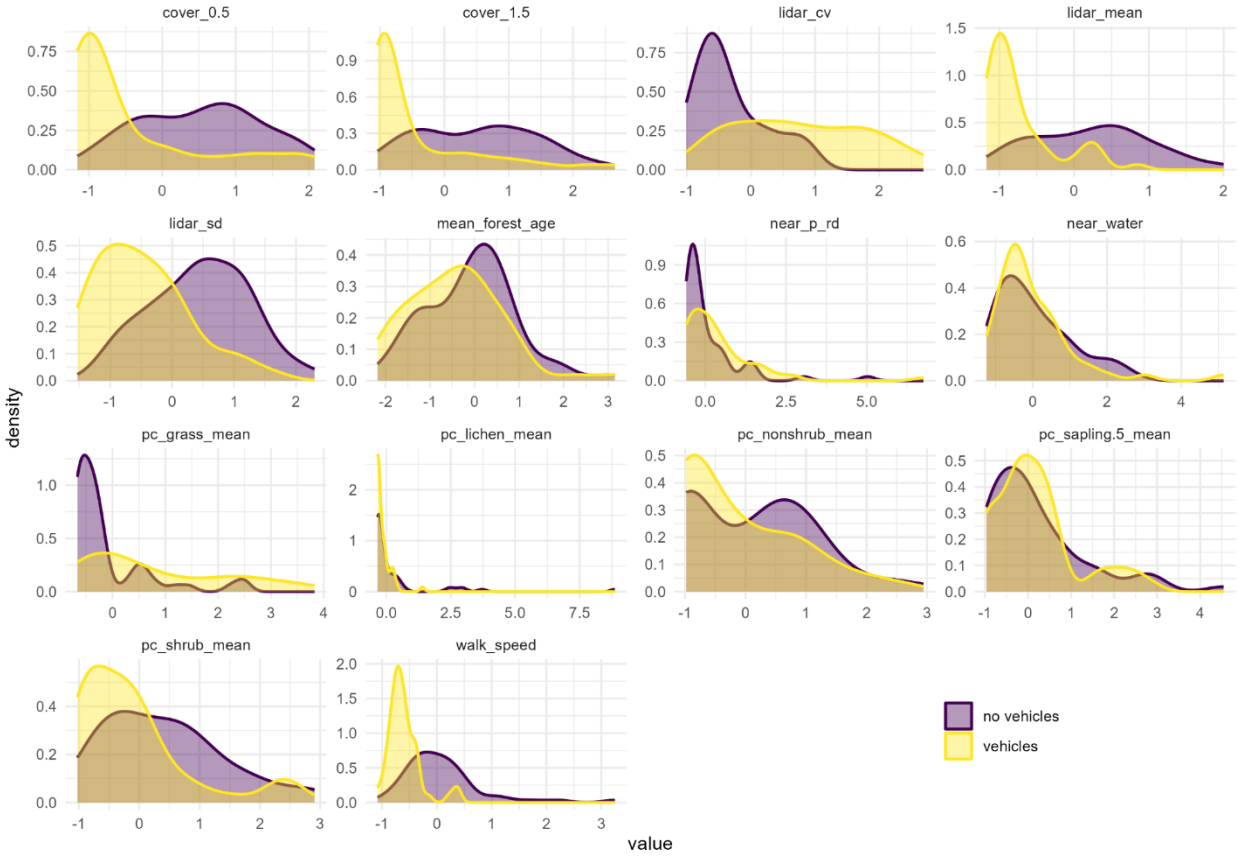

Figure A3. Distributions comparing standardized characteristics of roads with and without vehicle traffic. Panels from top left to bottom right show percent hiding cover a 0.5 m height, percent hiding cover at 1.5 m height, coefficient of variation of vegetation height over 100 m, mean vegetation height over 100 m, standard deviation of vegetation height over 100 m, mean age of surrounding forest within 100 m radius, distance to nearest primary road, distance to nearest waterbody, percent grass cover, percent lichen cover, percent forb cover, percent sapling cover, percent shrub cover, and time to walk 50 m.