







ARTICLE

Disturbance-mediated changes to boreal mammal spatial networks in industrializing landscapes

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Abstract

Compound effects of anthropogenic disturbances on wildlife emerge through a complex network of direct responses and species interactions. Land-use changes driven by energy and forestry industries are known to disrupt predator–prey dynamics in boreal ecosystems, yet how these disturbance effects propagate across mammal communities remains uncertain. Using structural equation modeling, we tested disturbance-mediated pathways governing the spatial structure of multipredator multiprey boreal mammal networks across a landscape-scale disturbance gradient within Canada's Athabasca oil sands region. Linear disturbances had pervasive direct effects, increasing site use for all focal species, except black bears and threatened caribou, in at least one landscape. Conversely, block (polygonal) disturbance effects were negative but less common. Indirect disturbance effects were widespread and mediated by caribou avoidance of wolves, tracking of primary prey by subordinate predators, and intraguild dependencies among predators and large prey. Context-dependent responses to linear disturbances were most common among prey and within the landscape with intermediate disturbance. Our research suggests that industrial disturbances directly affect a suite of boreal mammals by altering forage availability and movement, leading to indirect effects across a range of interacting predators and prey, including the keystone snowshoe hare. The complexity of network-level direct and indirect disturbance effects reinforces calls for increased investment in addressing habitat degradation as the root cause of threatened species declines and broader ecosystem change.

KEYWORDS

camera trapping, community ecology, context dependency, disturbance, ecological networks, predator, prey, structural equation modeling

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INTRODUCTION

To effectively combat the impacts of environmental change on biodiversity, the conservation focus should broaden from single species and sites to ecological networks (Harvey et al., 2017). Anthropogenic disturbance affects wildlife through a combination of heterogeneous species' responses to stressors (Heim et al., 2019; Suraci et al., 2021) and complex networks of species interdependencies (e.g., predation, competition) that vary across space and time (Dorresteijn et al., 2015; Tyliaakis et al., 2008). Yet, contemporary conservation targets tend to simplify complex multipredator multiprey mammalian systems (Montgomery et al., 2019), which precludes understanding of the mechanisms by which widespread landscape change affects mammalian biodiversity. A detailed understanding of how disturbance propagates across mammalian ecological networks can help managers move beyond a narrow focus on threatened species (proximate value) to target mechanisms underlying changes to ecological processes (ultimate value).

Disturbances from the energy and forestry industries in western Canada's oil sands region have modified boreal forests at rates with few analogs (Pickell et al., 2015), causing impacts on wildlife that are exemplified by the conservation challenges faced by threatened woodland caribou (*Rangifer tarandus caribou*), a flagship species for boreal biodiversity (Hebblewhite, 2017). Linear (e.g., roads, seismic lines) and block (or polygonal, e.g., well sites, harvest cutblocks) disturbance features are considered the ultimate mechanisms of the persistent decline of boreal caribou populations (Johnson et al., 2020). Notably, caribou population declines have been proximally attributed to altered predation dynamics driven by the indirect effects of habitat disturbance (Serrouya et al., 2021). Linear disturbances facilitate wolf (*Canis lupus*) movement and decrease prey search times (Dickie et al., 2017). Concurrently, the conversion of mature forest to early-seral vegetation in both linear and block features provides forage subsidies to primary ungulate prey (white-tailed deer *Odocoileus virginianus* and moose *Alces alces*; Fisher et al., 2020, 2021), which sustain larger wolf populations. These act synergistically to increase wolf predation to unsustainable rates on caribou via disturbance-mediated apparent competition (Wittmer et al., 2005). Conservation initiatives have thus focused primarily on combating the proximate cause of caribou declines by reducing wolf and primary prey populations (Hervieux et al., 2014; Serrouya et al., 2015) with more limited efforts to halt habitat loss as the ultimate driver (Nagy-Reis et al., 2021).

The impacts of landscape change in western boreal forests extend, however, well beyond the wolf-caribou

paradigm. Fisher and Burton (2018) suggested that differential responses of boreal mammals to anthropogenic disturbances promote an intricate landscape of wildlife winners and losers. Disturbance-induced movement and prey subsidies can benefit a large suite of boreal predators other than wolves, including black bears (*Ursus americanus*), cougars (*Puma concolor*), coyotes (*Canis latrans*), and lynx (*Lynx canadensis*), potentially increasing predation pressure on caribou in an additive manner (Fisher & Burton, 2018). Variable responses by predators to disturbance may, however, simultaneously shape agonistic encounters between dominant and subordinate species, or alter carrion provisioning patterns, with potential cascading effects (Prugh & Sivy, 2020; Ritchie & Johnson, 2009). Multipredator responses may also be influenced by understudied impacts of industrial development on alternative prey species of high biomass such as the snowshoe hare (*Lepus americanus*) (Boutin et al., 1995). Novel disturbance-mediated dynamics within and across predator and prey guilds are thus likely to lead to community-level structural shifts (Wittische et al., 2021) that are overlooked in contemporary management approaches to species-at-risk (Fisher & Burton, 2018).

Despite the call for community focus, community-level inference in the oil sands has been based on studying species independently (Toews et al., 2018), pooling species into guilds (Wittische et al., 2021), or describing pairwise interspecific dependencies (Tattersall et al., 2020). Integrated multispecies assessments are in their infancy (Beirne et al., 2021). Importantly, conventional multivariate procedures attempt to isolate disturbance effects rather than parse out indirect relationships predicted by the interplay between disturbance-induced subsidies and predatory/competitive dynamics (but see Fisher & Ladle, 2022). Path analysis approaches, such as structural equation modeling (SEM), that encode causal hypotheses about system dynamics provide an alternative and promising avenue for integrated evaluation of competing ecological hypotheses about direct and indirect effects of disturbance among multiple species (Addicott et al., 2022; Grace, 2008; Wilson et al., 2021). In other words, SEMs not only provide a way to better understand the myriad interactions species may have with one another, but SEMs could also help identify whether disturbance could modulate and propagate across those interactions.

We explored disturbance-mediated pathways governing the emergent spatial structure of multipredator multiprey boreal mammal networks across three landscapes within the oil sands of northeastern Alberta, Canada. Analyzing camera-trapping data within an SEM framework, we investigated how site use intensity relates to linear and block disturbances across a landscape-scale gradient of

industrial disturbances, both directly and indirectly via interspecific spatial dependencies (spatial patterns of co-occurrence or segregation compatible, or not, with predicted interactions). Our focal assemblage was a subset of large- and medium-sized boreal mammal species that have documented associations with industrial disturbances and well-established competitive and predatory dynamics: wolf (apex predator), black bear

and coyote (generalist subordinate predators), lynx (specialist subordinate predator), moose and white-tailed deer (primary large prey), snowshoe hare (primary small prey), and caribou (secondary large prey and flagship species). We developed an *a priori* theoretical model (Figure 1, Table 1) to explore the following set of nonexclusive hypotheses on the compound effects of disturbance on boreal mammal spatial networks:

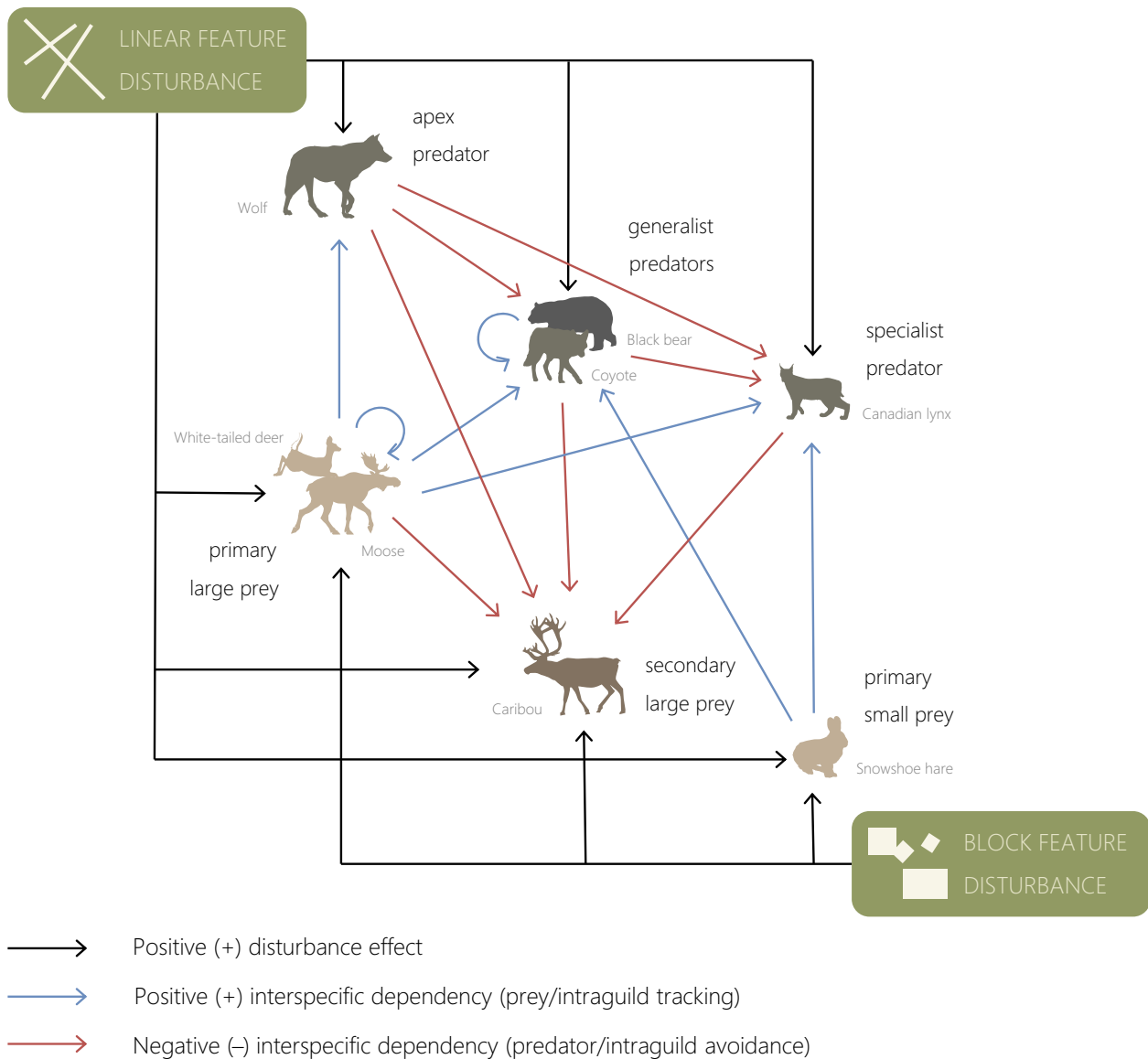


FIGURE 1 *A priori* model illustrating the hypothesized direct and indirect, via interspecific dependencies, effects of disturbance features on boreal mammal site use intensity (see Table 1). Pathways in the network are either direct effects: single link between disturbance variables (exogenous predictor) and species site use (endogenous response variable); or indirect effects: two consecutive links between a disturbance variables and species site use via a single mediating species (endogenous predictor). For example, linear disturbance features have a predicted direct effect on primary prey species (one arrow from disturbance to prey species), and an indirect effect on predator species (second arrow in the same direction between the prey and predator species) due to spatial dependencies of predators on primary prey.

TABLE 1 Predictor and response variables used to model direct and indirect effects of disturbance features on boreal mammal site use intensity under a structural equation model (SEM) framework.

Category	Type	Variable	Units (range)	Source	Description	Rationale
Mammal site use and interspecific dependencies	Endogenous (response and predictor)	Site use intensity	Independent detections <30 min (0–150)	Camera-trap data	Species-by-site count data for wolf, black bear, coyote, lynx, moose, white-tailed deer, snowshoe hare, and caribou.	Boreal mammal site use intensity is influenced by disturbance features and interspecific dependencies associated with predatory (prey tracking and predator avoidance) and intraguild (suppression and facilitation among predators, resource dominance and apparent competition among prey) dynamics.
Linear and block disturbance features	Exogenous (predictor only)	Linear feature density (lf)	km/km ² (0–21.7)	ABMI (2019)	Remote-sensed measures of total line density of seismic lines, pipelines, transmission lines, and gravel roads in the camera site surroundings.	Linear corridors cleared of vegetation for oil and gas exploration and transporting, electrical transmission lines or vehicle roads, are used by predators for movement and hunting, and used by prey to exploit early-seral vegetation subsidies on corridor sides (including caribou during summer; Denryter et al., 2017).
		On- or off-line (online)	Binomial (0/1)	Survey design	On- or off-line camera placement.	
		Block feature cover (bf)	km ² (0–2.88)	ABMI (2019)	Remote-sensed measures of the cumulative cover of well sites and forest harvest cutblocks in the camera site surroundings.	
Baseline habitat preferences	Exogenous (predictor only)	Wetland probability (wp)	Probability (0.03–0.94)	Hird et al. (2017)	Remote-sensed estimates of average probability of wetland in the camera site surroundings.	Broad proxy for habitat composition driving main species–habitat relationships in western Canada's boreal forests.

H1. Direct effects. Disturbance-induced movement and forage subsidies directly and positively influence all focal species, not only wolves and their primary prey. We predicted that site use intensity of predators is directly and positively associated with linear disturbances because of travel subsidies and increased hunting success. Similarly, we expected site use intensity of prey species to be directly and positively associated with linear and block disturbances because of

the conversion of mature forest to early-seral vegetation.

H2. Indirect effects. Multispecies responses to disturbance precipitate complex additive or contrasting effects via interspecific dependencies associated with predatory and intraguild dynamics. We predicted that predators' site use is indirectly associated with disturbance features as they are tracking increased site use by their primary prey.

Conversely, increased movement and prey tracking by predators on disturbance features create higher predation-risk areas that are avoided by caribou (secondary prey). Additionally, we predicted that indirect disturbance effects propagate through intraguild dynamics, namely via suppressive or facilitative interactions between predators and resource dominance and/or apparent competition among prey species.

H3. Context-dependent effects. Disturbance effects are context-dependent according to the overall degree of landscape disturbance. We identified two nonexclusive predictions about context-dependency. Disturbance-mediated effects on mammal site use may be more pronounced at low or medium anthropogenic disturbance due to the potential spatial saturation of disturbances and resource subsidies in the most disturbed landscape; and/or, disturbance-mediated effects may predominantly manifest in the most disturbed landscapes where disturbance has exceeded presumable, albeit

unknown, thresholds needed to induce spatial responses.

METHODS

Study areas

Our study was carried out across three boreal forest landscapes within the Athabasca oil sands region in north-eastern Alberta, Canada (Figure 2). Extensive petroleum exploration and extraction features coupled with forestry activities permeate the entire region, with considerable variation in the local intensity of disturbances from land use. The three focal study areas comprise a gradient of industrial development, with low (LD; Richardson 57.8° N 110.9° W), medium (MD; Algar 56.3° N 112.5° W), and high (HD; Christina Lake 55.6° N 110.9° W) levels of landscape-scale disturbance, that is, increasing seismic line density, petroleum extraction operations, and timber harvesting. Study area details are provided in Appendix S1.

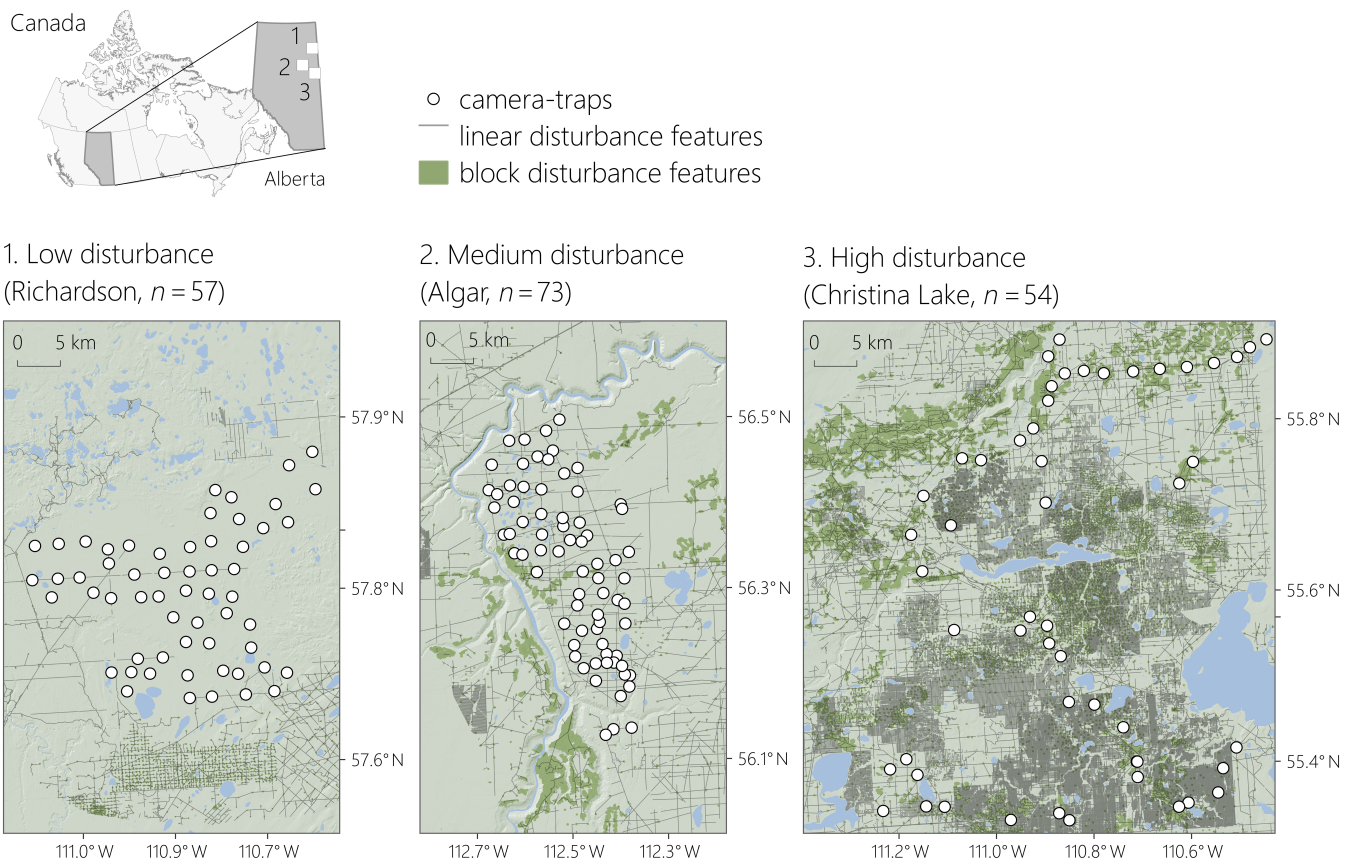


FIGURE 2 Camera-trapping surveys conducted across a landscape gradient of industrial development in the Athabasca Oil Sands Region in Northeast Alberta, Canada, with increasing amounts of linear and block disturbance features.

SEM framework

We adopted a piecewise SEM approach to evaluate hypothesized pathways governing the direct and indirect effects of disturbance (exogenous predictor variables) on focal boreal mammals' site use intensity (endogenous response and predictor variables) (Figure 1). SEM departs from traditional linear modeling by explicitly considering pathways in the model as hypothesized causal relationships, based on pre-existing knowledge of the focal system, and treating variables as both responses and predictors. This allows for quantification of both direct and indirect effects otherwise unrecognized in a single model (Grace, 2008). Piecewise (or "local") SEMs are based on graph theory whereby a set of linear equations translate the path diagram and are solved individually (Lefcheck, 2016).

Mammal site use intensity data (endogenous variables)

We used camera-trap detection data to describe patterns of site use intensity (counts at sampling sites) of focal boreal mammals. This measure reflects both the local abundance of animals and their movements or use of habitat features within their home range (Johnson, 1980). We assumed that variation in detections reflects the ecological signal of interest beyond observation error (see Appendix S2 for further discussion). We compiled data from 184 camera-trap sites deployed across the three study areas between 2016 and 2021; $n = 57$ for Richardson (2018–2021), $n = 73$ for Algar (2016–2019), and $n = 54$ for Christina Lake (2020–2021). The number of operational camera sites varied over time (Appendix S2: Table S1). Out of the 184 unique sites, 41% were surveyed for ≤ 2 years ($n = 75$), 35% for 3 years ($n = 65$), and 24% for 4 years ($n = 44$), with such proportions varying across landscapes. We only used survey data collected between April and September of each year, corresponding to the mostly snow-free vegetation growing season. Sites were spaced, on average, 2.12 ± 1.04 km apart (2.48 ± 0.43 Richardson, 1.44 ± 0.58 Algar, 2.58 ± 1.40 Christina Lake) according to stratified random designs specific to each area (details in Appendix S2).

To extract site count data, images were classified to species level and grouped into "independent detections" using a 30-min time window. Because we used data from multiple years and surveys, we created a "stacked design" by treating camera site-year combinations as the sampling unit. Hence, our endogenous variables (response or biotic predictor) were sample unit specific counts of all independent detections for each species, hereafter site use

intensity. The combined survey effort across the three study areas totaled 517 camera site-by-year sampling periods, 68,976 trap days, and 10,479 independent detections of eight focal species (Appendix S2: Tables S1 and S2).

Disturbance and environmental data (exogenous variables)

We derived the amount of linear and block feature disturbance for each camera site from the Alberta Biodiversity Monitoring Institute (ABMI) 2019 Human Footprint Map Enhanced for Oil Sands Monitoring Region (Table 1). We collected disturbance variables within 500, 1000 and 1500 m radii circular buffers around each camera site, and conducted a preliminary sensitivity analysis to identify the most parsimonious scale for each variable (Fisher et al., 2011) (Appendix S3). Linear feature disturbance was measured as the total line density (in kilometers per square kilometer) of seismic lines, pipelines, transmission lines, and gravel roads in the site buffer (1500 m radius). We additionally considered an "on-/off-line" binary variable to account for animal use of cameras placed on linear features (although no cameras were placed on lines in the high-disturbance landscape). Block feature disturbance was measured as the cumulative cover (in square kilometers) of well sites and forest harvest cutblocks in the camera buffers (1500 m radius). In addition to disturbance features, we sought to consider the underlying effect of dominant species-habitat relationships (Fisher & Burton, 2018). We used remote-sensed estimates of the average probability of wetland (Hird et al., 2017) in the site vicinity (500 m radius) as a proxy for habitat composition in the boreal forest, namely differences between lowland hydric areas and mesic upland sites (Beirne et al., 2021). Prior to modeling, we ensured no strong collinearity between covariates by evaluating pairwise correlations ($|r| > 0.7$).

SEM implementation

We implemented a single SEM translating our *a priori* model using site-specific disturbance features and wetland habitat as exogenous variables (Figure 1) and species' count data as endogenous (response and predictor) variables. To formally test for context-dependency across landscapes, we implemented the "multigroup" formulation of the piecewise SEM with "landscape" as a categorical grouping variable (low, medium, and high disturbance), using the functions "psem" and "multigroup" in R package *piecewiseSEM* (Lefcheck, 2016). This approach introduces a model-wide interaction term to identify whether allowing

landscape-specific pathways improves the quality of the model. Specifically, if the interaction is significant the path coefficient can vary by landscape (hereafter “context-dependent effect”); otherwise the estimation is fixed across all landscape-levels (hereafter “consistent effect”). SEM formulation details are reported in Appendix S4.

Direct and indirect effects were extracted from path coefficient estimates from the univariate regressions. To assess H1, direct pathways between disturbance variables (exogenous predictor) and species site use (endogenous response variables) were considered as direct effects. For H2, pathways separated by one mediating species (endogenous predictor) were considered as indirect effects and measured as the product of the two direct path coefficients; that is, between the exogenous and endogenous predictor variables, and between the endogenous predictor and response variables. For an indirect effect to be considered significant, both individual connecting paths had to be significant at the 5% level (p -value ≤ 0.05). For H3, the significance of the landscape interaction term associated with each effect pathway informed the evidence in support of context-dependency. Given the complexity of our analysis, we prioritized assessing the emergence (i.e., significance and relative directionality) of specific pathways over quantifying their effect sizes. We present unstandardized effect coefficients for comparing specific pathways under our multiarea inference objectives; we do not report standardized coefficients because their interpretation would be made difficult by different variances between landscapes (hindering pathway comparability) and the potential influence of species traits (e.g., body size, movement) on detection rates and ecological interpretation of effect sizes.

RESULTS

The initial SEM representing hypotheses about the compound effects of disturbance on boreal mammal spatial networks failed to fit the data adequately (Fisher’s $C = 24.52$, $df = 14$, p -value = 0.04). Using conditional separation tests to identify missing statistically important paths (Lefcheck, 2016), we additionally considered the direct effect of block disturbances on black bear site use intensity. The resulting model fitted the data well (Fisher’s $C = 6.211$, $df = 12$, p -value = 0.91; Figure 3). Below we present effect estimates, decomposed into direct and indirect components, using the following notation: “exogeneous predictor variable” \rightarrow (“endogenous predictor variable” \rightarrow) “endogenous response variable” (“coefficient estimate”^{“landscape”}). See Figure 1 for an

example of how direct and indirect effects are interpreted. Individual path coefficients are presented in Appendix S4: Table S1.

Direct disturbance effects (H1)

Linear disturbances (measured as linear density [lf] and “online” site use [online]) had pervasive, and mainly positive, direct effects on-site use intensity for all focal species except caribou in at least one of the landscapes (Figure 3, Table 2). The influence of block disturbances [bf] was less pervasive, with only negative direct effects observed for three focal species (bear, moose, caribou; Figure 3, Table 2).

Among predator species, only black bears exhibited a negative and consistent (“c” indicates consistent effects across landscapes) association with linear feature density ($lf \rightarrow bear[-0.05^c]$). Linear disturbances had positive and consistent effects on wolf and lynx; wolves used “online” sites more than “off-line” ($online \rightarrow wolf[2.27^c]$) whereas lynx used sites with higher surrounding linear feature density more intensively ($lf \rightarrow lynx[0.09^c]$). Coyotes responded positively to linear disturbances in only the medium disturbance landscape ($lf \rightarrow coyote[2.68^{MD}]$). Linear disturbances were also significant predictors of site use by primary prey species. White-tailed deer and moose exhibited a consistent, positive association with “online” sites ($online \rightarrow deer[0.65^c]$; $online \rightarrow moose[0.43^c]$), while snowshoe hares had lower use of “online” sites in the low disturbance landscape ($online \rightarrow hare[-3.61^{LD}]$). For all three primary prey, site use was positively influenced by line density in the medium disturbance landscape ($lf \rightarrow deer[0.71^{MD}]$, $lf \rightarrow moose[0.75^{MD}]$, $lf \rightarrow hare[1.93^{MD}]$). By contrast, line density in the high disturbance landscape had a negative influence on white-tailed deer site use ($lf \rightarrow deer[-0.04^{HD}]$). The negative effects of block disturbances were consistent among study landscapes. Site use was lower with increasing block disturbance for one predator species, black bear ($bf \rightarrow bear[-0.66^c]$), and two large prey species, moose ($bf \rightarrow moose[-0.72^c]$) and caribou ($bf \rightarrow caribou[-1.20^c]$).

Indirect disturbance effects (H2)

SEM results underscored the importance of considering the indirect effects of disturbance acting through inter-specific dependencies. Linear disturbances indirectly affected the site use of five species in at least one landscape (Figure 3, Table 2). Indirect effects were mainly mediated by positive spatial dependencies between

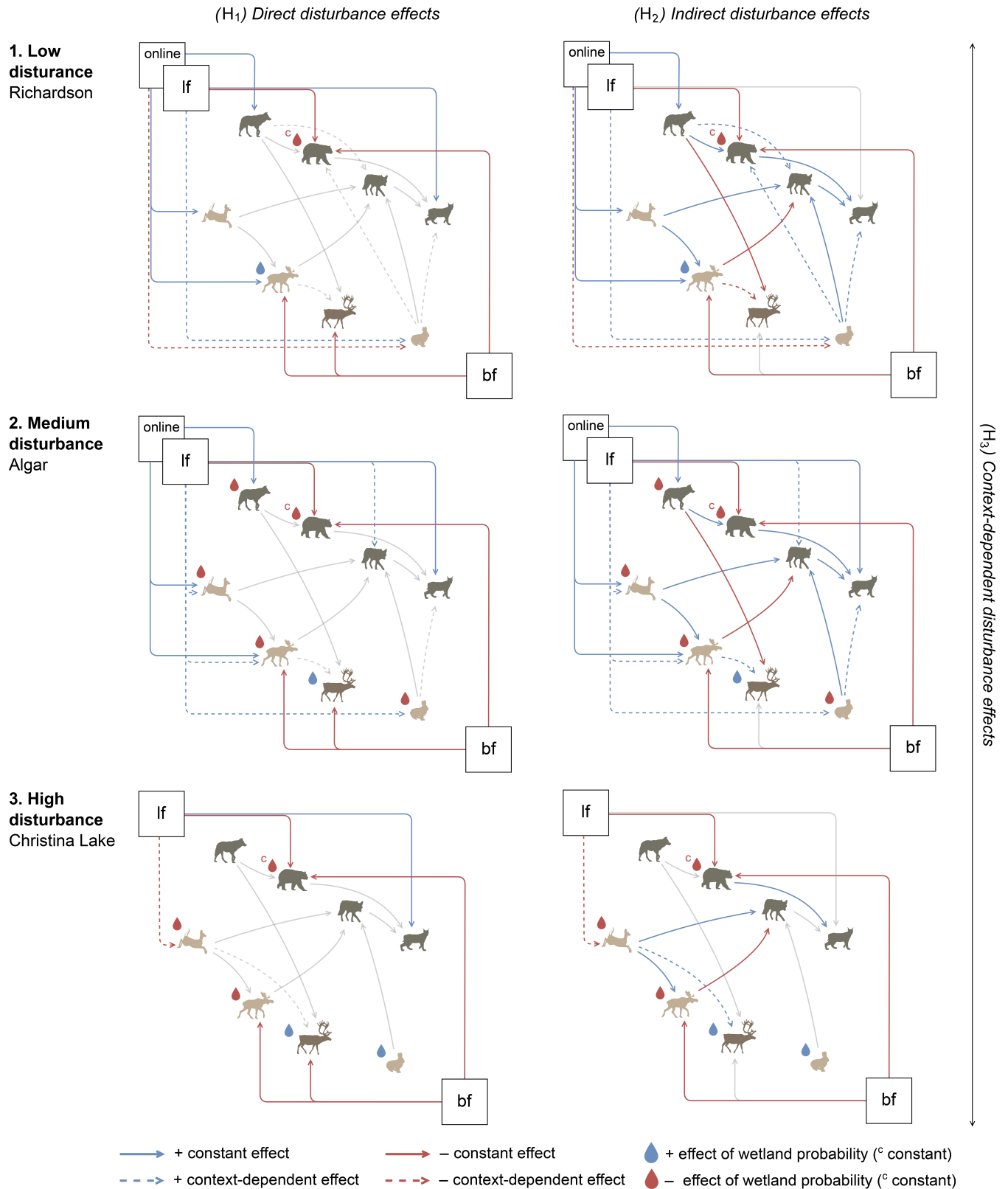


FIGURE 3 Structural equation model (SEM) evaluating direct and indirect effects of linear feature (density [lf] and “online” site use [online]) and block feature (cover [bf]) disturbance on boreal mammal site use intensity. Only significant pathways (p -value ≤ 0.05) are shown for increased clarity. For ease of interpretation, direct (H₁) and indirect (H₂) effects are presented separately by gray-shading other pathways, although both are extracted from a single set of model results. Individual path coefficients are presented in Appendix S4: Table S1.

TABLE 2 Structural equation modeling unstandardized path coefficient estimates for direct and indirect effects of linear and block disturbance features on boreal mammal species site use intensity patterns.

Exogeneous predictor variable	Endogenous response variable	Direct effects	Indirect effects (→ endogenous predictor variable)					
			→ Wolf	→ Bear	→ Coyote	→ Moose	→ Deer	→ Hare
Linear feature density (1500 m radii buffers)	Wolf	
	Bear	-0.05 ^c	1.02 ^{LD}	
	Coyote	0.82 ^{LD}	
	Lynx	2.68 ^{MD}	0.02 ^{MD}	0.24 ^{MD}	
	Moose	0.09 ^c	...	-0.004 ^c	0.17 ^{MD}	...	-0.001 ^{HD}	
	Deer	0.75 ^{MD}	0.01 ^{MD}	
	Caribou	0.71 ^{MD}	-0.001 ^{HD}	
	Hare	-0.04 ^{HD}	0.07 ^{MD}	...	
Online	Wolf	6.57 ^{LD}	
	Bear	1.93 ^{MD}	
	Coyote	2.27 ^c	
	Lynx	0.19 ^c	
	Moose	6.32 ^{LD}	-0.12 ^c	0.02 ^c	
	Deer	0.43 ^c	0.01 ^c	
	Caribou	0.65 ^c	
	Hare	-0.45 ^{LD}	-0.11 ^{LD}	0.04 ^{MD}	
Block feature cover percentage (1500 m radii buffers)	Wolf	-3.61 ^{LD}	
	Bear	
	Coyote	-0.66 ^c	
	Lynx	
	Moose	-0.05 ^c	...	0.20 ^c	...	
	Deer	-0.72 ^c	
	Caribou	-1.20 ^c	0.18 ^{LD}	
	Hare	-0.07 ^{MD}	

Note: Coefficients are unstandardized (required for multiarea inference) and thus not comparable across different pathways. Only significant effects (p -value ≤ 0.05) are shown for increased clarity (see Appendix S4: Table S1 for individual coefficient estimates). “^c” indicates consistent effects across landscapes. Context-dependent coefficients are presented by landscape: ^{LD} low disturbance (Richardson), ^{MD} medium disturbance (Algar), ^{HD} high disturbance (Christina Lake). “...” indicates pathways not considered in the model (see Figure 1).

subordinate predators and primary prey, positive dependencies among predators, and variable dependencies among large prey. The fewer direct effects of block disturbances extended to a smaller set of indirect pathways, affecting only two species (Figure 3, Table 2).

Linear disturbances had indirect, but variable, effects on all subordinate predators as mediated by dependencies with primary prey, that is, prey tracking (deer → coyote[0.03^c], hare → bear[0.16^{LD}], hare → coyote[0.12^c], hare → lynx [0.19^{LD}/0.10^{MD}]). Positive indirect effects manifested through a combination of positive direct effects of linear disturbances

on prey and positive predator–prey spatial dependencies (online \rightarrow deer \rightarrow coyote[0.02^c], lf \rightarrow deer \rightarrow coyote [0.02^{MD}], lf \rightarrow hare \rightarrow bear[1.02^{LD}], lf \rightarrow hare \rightarrow coyote [0.82^{LD}/0.24^{MD}], lf \rightarrow hare \rightarrow lynx[1.22^{LD}, 0.19^{MD}]). The negative indirect effects acted through negative direct responses of prey to linear disturbances (online \rightarrow hare \rightarrow bear[−0.56^{LD}], online \rightarrow hare \rightarrow coyote[−0.45^{LD}], online \rightarrow hare \rightarrow lynx[−0.67^{LD}], lf \rightarrow deer \rightarrow coyote[−0.001^c]) or an unpredicted negative predator–prey dependency of coyote on moose (online \rightarrow moose \rightarrow coyote[−0.12^c]). Remarkably, no significant spatial dependencies were found between wolves and primary prey, and hence no evidence for indirect disturbance effects on the apex predator. However, wolves were the only predator species inducing a consistent negative response by caribou, that is, predator avoidance (wolf \rightarrow caribou[−0.20^c]); in turn mediating a negative and consistent indirect effect of linear features on caribou via wolf's increased use of “online” sites (online \rightarrow wolf \rightarrow caribou[−0.45^c]).

Indirect effects of linear disturbances also propagated in the spatial network through intraguild dependencies, that is, predator–predator and prey–prey associations. Positive dependencies between dominant and subordinate predators mediated indirect effects of linear features on all nonapex predators; mainly positive (online \rightarrow wolf \rightarrow bear[0.19^c], online \rightarrow wolf \rightarrow coyote [6.32^{LD}], lf \rightarrow coyote \rightarrow lynx[0.17^{MD}]) but also negative (lf \rightarrow bear \rightarrow lynx[−0.004^c]) depending on the dominant predator's direct association with linear disturbance. Positive spatial dependencies among large primary prey (deer \rightarrow moose[0.01^c]) mediated indirect effects of linear features on moose, depending on deer's response to linear disturbance across contexts (online \rightarrow deer \rightarrow moose [0.01^c], lf \rightarrow deer \rightarrow moose[0.01^{MD}, −0.001^{HD}]). Finally, indirect effects of disturbance on caribou site use intensity also occurred via variable spatial dependencies with one of its (apparent) competitors, moose, at low and medium disturbance landscapes (moose \rightarrow caribou[−0.25^{LD}, 0.10^{MD}]). Coupled with direct responses of moose to linear (positive) and block (negative) disturbances, these dependencies translated into context-dependent, indirect effects over caribou at low and medium disturbance landscapes; both positive (online \rightarrow moose \rightarrow caribou[0.04^{MD}], lf \rightarrow moose \rightarrow caribou[0.07^{MD}], bf \rightarrow moose \rightarrow caribou[0.18^{LD}]) and negative (online \rightarrow moose \rightarrow caribou[−0.11^{LD}], bf \rightarrow moose \rightarrow caribou[−0.07^{MD}]).

Context-dependent disturbance effects (H3)

All direct effects of block feature disturbance ($n = 3$) were consistent across landscapes whereas half of

10 observed direct effects of linear disturbance were context-dependent, either exclusive to a single landscape context ($n = 3$) or with varying coefficient across landscapes ($n = 2$; Figure 3, Table 2). Consistent linear disturbance effects prevailed among predators (except coyotes), while context-dependent responses were common among prey species. The association of mammals with “online” sites was consistent for all species except hares, whereas primary prey responses to linear feature density were context-dependent. Effects of linear feature density prevailed in the medium disturbance landscape, with context-specific responses of four species (coyote, deer, moose, hare). In low- and high-disturbance landscapes, only one prey species (hare and deer, respectively) was significantly influenced by linear feature density whereas all others exhibited neutral responses. At low overall disturbance, hares maintained a positive, but weaker, association with linear feature density. At high disturbance, the influence of linear feature density on deer shifted from positive to negative. Hare was the only other species exhibiting a similar shift in effect direction, with a negative association with “online” sites at low disturbance but positive in the medium disturbance landscapes. This variation in direct responses of deer and hare to linear feature disturbance induced strong context-dependency of indirect pathways affecting predator species. Notably, the influence of hares on predators decreased with increasing landscape-level disturbance, both in number and strength of significant effects. Most other interspecific dependencies were consistent across landscapes.

DISCUSSION

The compound effects of anthropogenic disturbances on spatial networks of predators, prey, and competitors, emerge as a mechanism behind the mammalian “winners and losers” observed in the developing western boreal forest (Fisher & Burton, 2018). As hypothesized, linear and block disturbances directly (H1) and indirectly (H2) affected patterns of space use for multiple predator and prey species. Direct disturbance pathways suggest most boreal mammals exploit the movement and forage subsidies provided by disturbances. Interspecific spatial dependencies affect, and are affected by, indirect disturbance pathways. We contend that disturbance-mediated predatory and intraguild dynamics facilitate both additive and contrasting impacts with community-level consequences beyond those implicated in the current wolf–caribou apparent competition paradigm. Importantly, in accordance with H3, we found that effects pathways are often context-dependent, varying with the overall degree of landscape disturbance. Our research highlights the

importance of community interactions as mechanisms for biodiversity loss, and the need to protect ecological networks of species interactions to achieve pressing conservation management goals.

Direct effects: Community-wide associations with linear but not block disturbances (H1)

The movement and forage subsidies provided by anthropogenic features are widely proposed mechanisms underlying the direct responses of boreal mammals to industrial landscape change. Although these are better understood for wolves (Dickie et al., 2017) and their primary prey (Laurent et al., 2021), these disturbance subsidies may be similarly exploited by other species (Fisher & Burton, 2018; Fisher & Ladle, 2022). As predicted, we detected a positive direct effect of linear features on most species' site use in at least one landscape. Wolves, coyote, and lynx, may make similar functional use of linear corridors to move faster and further through the otherwise high-resistance boreal forest surface, increasing prey search rates (Dickie et al., 2017). Contrastingly, but in accordance with previous findings (Fisher & Ladle, 2022), black bear site use was negatively associated with linear feature density. Large (moose and white-tailed deer) and small (snowshoe hare) primary prey also exhibited predominantly positive direct associations with linear disturbances. Boreal ungulates travel linear corridors on which they exploit the early-seral vegetation subsidies (Darlington et al., 2022; Dickie et al., 2020). Unrestored lines maintain early-seral vegetation long after disturbance and provide more important forage relative to the forest matrix (Dabros et al., 2018). Our results suggest that smaller herbivore species like the snowshoe hare might also be attracted to forage subsidies from increasing edge habitat and gap dynamics (Hodson et al., 2010).

Unexpectedly we detected fewer, and negative, associations between boreal mammals and block disturbances, despite increased early-successional forage. Caribou's negative response is consistent with diminished lichen availability (Nagy-Reis et al., 2021). While positive selection of cutblocks and other polygonal features by other large ungulates has been described, mammal responses to boreal forest clearings are dynamic in relation to successional stage and nature of disturbance (Fisher & Wilkinson, 2005) and likely reflect complex trade-offs between resource acquisition and the perception and avoidance of predation risk (McKay & Finnegan, 2022). These nuanced aspects of block disturbance effects might have weakened expected positive responses. It is likely, however, that demographic responses

to forage subsidies (i.e., increased survival and reproduction) prevail over changes in space use (Fisher & Wilkinson, 2005).

Indirect effects: Interspecific dependencies mediate disturbance pathways (H2)

We detected an interplay between direct responses to disturbance and interspecific dependencies associated with predatory and intraguild dynamics. These indirect effects of disturbance influenced most species, either adding to or counteracting the direct effects. In partial accordance with the classic wolf-caribou paradigm (Serrouya et al., 2021), caribou association with linear disturbances was mediated by spatial dependencies with its primary predator, wolf, and apparent competitor, moose. Caribou avoided lines used by wolves probably as a result of increased predation risk (Mumma et al., 2018). However, we did not detect expected spatial dependencies between wolves and their primary prey, suggesting wolves may select favorable hunting conditions in linear features rather than track prey relative abundance. Alternatively, predator-avoidance behaviors may mask predicted prey-tracking spatial signatures. Caribou site use was also lower at online sites used more by moose in the low disturbance landscape (see *Context-dependency hinders extrapolation of disturbance effects (H3)*), in accordance with spatial partitioning patterns predicted by competition and shared predation risk (Cumming et al., 1996). Caribou did not display similar segregation from white-tailed deer in any landscape, which warrants further investigation. The range expansion of deer into the boreal forests of North America (Dawe & Boutin, 2016) may have occurred too recently for caribou to recognize this species as an indicator of predation risk.

Remarkably, most indirect disturbance effects propagated via pathways that are typically overlooked; namely, intraguild associations among predators, and prey tracking by subordinate predators. Research on carnivore associations often focuses on avoidance behaviors (Ritchie & Johnson, 2009). In contrast, we show positive spatial dependencies among predators. The use of linear features by dominant carnivores was typically linked to their use by subordinate counterparts; potentially because of facilitative interactions, such as carrion provisioning (Prugh & Sivy, 2020), or shared responses to unmeasured ecological cues (e.g., linear feature characteristics; Tattersall et al., 2020). Spatial dependencies of subordinate predators with primary prey (deer and hare) were also key mediators of indirect effects of linear disturbances. Coyotes often prey on white-tailed deer (Lingle, 2002) and tracked this species' use of linear

features. Hare availability is important for several boreal predators (Boutin et al., 1995); locations with higher linear feature density were exploited by hares, and in turn by lynx (specialist hare predator), coyote and black bear (facultative hare predators).

Insights from indirect disturbance pathways are relevant for current species-at-risk policy and broader efforts to conserve ecological networks. Our results support the notion that caribou respond to increased risk of wolf predation in and around linear features (Dyer et al., 2001). A key insight is that the direct and indirect effects of disturbance—that is, facilitated movement and access to primary prey, respectively—influence several secondary predators of caribou and thus presumably increase predation pressure, particularly on caribou neonates (Lewis et al., 2017). Caribou do not seem to avoid these other predators, potentially increasing encounter frequency, and thus overall predation risk, particularly given positive spatial dependencies among predators. However, among-predator associations fostered by linear disturbances might enhance agonistic encounters rather than benefiting subordinate predators (Chow-Fraser et al., 2022; Prugh & Sivy, 2020). Moreover, contrasting responses of black bears to disturbance features might promote complex predator-avoidance trade-offs. Caribou adopting habitat selection strategies to reduce predation risk from predators using linear features, like wolves, may in turn face increased predation by bears (Leblond et al., 2016).

A second key insight from our study is that the caribou-predator dynamic may be indirectly linked to another dominant process in boreal systems: the snowshoe hare cycle (Krebs et al., 2001). Disturbance-mediated increases in hares, as suggested by our results, could represent a prey subsidy for secondary caribou predators, thereby increasing overall predation pressure on caribou. Research on caribou and hare dynamics has been largely separate, yet the poorly understood responses of snowshoe hares to increasing anthropogenic disturbances, and knock-on effects on multiple predator species, are concerning considering the keystone role of hare population cycles on vertebrate communities (Boutin et al., 1995).

Context-dependency hinders extrapolation of disturbance effects (H3)

Context-dependency is increasingly acknowledged as a key aspect of ecological inference (Rollinson et al., 2021) including for species interactions (Bar-Massada & Belmaker, 2017; Chamberlain et al., 2014). Here, context-dependency underlined mammal spatial network structure across a gradient of industrial disturbance. Generally,

responses to linear features were consistent for predators, but often idiosyncratic for prey. A greater number of positive associations of prey with line density was detected in the medium disturbance landscape, potentially reflecting density-dependent and resource-dependent habitat selection (Avgar et al., 2020). This matches our initial predictions that disturbance-mediated effects would manifest above presumed disturbance thresholds but decrease with spatial saturation of disturbances, and has implications for effectively targeting linear restoration efforts. Variable interspecific dependencies across landscapes further contributed to context-dependency in indirect disturbance effects. For instance, caribou avoided moose only in the low disturbance landscape, where larger expanses of undisturbed habitat are available for segregation. Similarly, spatial dependencies between nonapex predators and primary small prey decreased with increasing landscape disturbance, potentially because of parallel density increases of alternative prey (Laurent et al., 2021).

Management implications and future directions

The complexity of network-level direct and indirect disturbance effects informs the debate surrounding the relative merits of managing species-at-risk population declines via predator and primary prey reductions (Hervieux et al., 2014; Serrouya et al., 2015) or restoring disturbed habitat (Beirne et al., 2021). Arguments have been advanced for lethal population control of predators and apparent competitors as a stop-gap solution to stem caribou population declines (Serrouya et al., 2019). However, we raise important questions regarding previously underemphasized cascading consequences for the wider community, as well as the inability of population reductions to address disruptions of other network pathways induced by habitat disturbances. Research is needed on the extent to which wolf control might release secondary predators from top-down suppression (Frey et al., 2022)—particularly if this suppression is currently enhanced by higher predator encounter rates on linear features—and on the implications for these predators of disturbance-mediated changes in snowshoe hares. There is also a need for increased investment in addressing habitat degradation as the ultimate cause of caribou declines and wider ecosystem change (Hebblewhite, 2017). Moreover, context-dependency underlies emergent patterns of disturbance effects, and likely associated ecological processes, underscoring that there will not be a “one-size-fits-all” solution. Understanding whether and how the overall disturbance level in a landscape dictates the effects of disturbance is important for identifying and prioritizing interventions, and avoiding

erroneous extrapolation of policy recommendations (Rollinson et al., 2021). Assessments of disturbance-mediated changes to ecological networks, conducted across a wider range of landscape gradients, and based on long-term monitoring and adaptive management strategies (see below), are needed to identify ecological thresholds and associated regulatory limits on disturbance (sensu Johnson, 2013) above which wildlife community dynamics may be fundamentally altered.

We highlight the value of a network approach to understanding biodiversity change in disturbed landscapes, but also the challenges. While the focus on emergent spatial patterns delivered valuable insights, it provided only limited understanding of underlying processes and demographic consequences of disturbance effects. Notably, by exploring interspecific dependencies, rather than interactions per se (Blanchet et al., 2020), it becomes difficult to interpret causality for pathways inconsistent with predicted interactions. Importantly, a holistic approach to ecological network research is limited by the level of complexity possible to accommodate in the model and the data available. Future studies would benefit from considering other rare but functionally important species (e.g., cougar, wolverine), heterogeneity in disturbance features (e.g., line type, forest stand age, recovery stage), and specific species–habitat relationships. Structural causal modeling, a novel extension to SEM, is a promising new approach for navigating such complexity (Arif & MacNeil, 2023). This method employs criteria to ascertain the statistical adjustments necessary for addressing causal queries in observational data, even in the presence of unobserved confounding variables.

We suggest that these conceptual and analytical approaches can be extended to investigate community-wide responses to management actions and global change drivers. By integrating management interventions, such as predator control and habitat restoration, with long-term wildlife community monitoring, longitudinal assessments of local network structure can elucidate how disturbance pathways and species dependencies are altered or restored by management (e.g., before-after-control experiments). Coordinated regional, multilandscape community monitoring offers an additional opportunity to scale up network inference to population- and regional-scale patterns (Wilson et al., 2021). Our SEM can be adapted to relate species-by-landscape population abundances to measures of landscape disturbance, management interventions, and other important environmental factors (e.g., climate). Ultimately, a transition toward ecological network research (Harvey et al., 2017) within an adaptive management framework (Burton et al., 2014) will be a crucial step in tackling the wicked problem of

biodiversity conservation on a rapidly changing planet (Defries & Nagendra, 2017).

AUTHOR CONTRIBUTIONS

A. Cole Burton, Joanna M. Burgar, Jason T. Fisher, and Emily J. Herdman were awarded funding to support this research. A. Cole Burton, Joanna M. Burgar, and Jason T. Fisher developed the multilandscape research design. A. Cole Burton, Jason T. Fisher and Emily J. Herdman managed the field operations. Gonçalo Curveira-Santos and A. Cole Burton conceived the ideas. Gonçalo Curveira-Santos analyzed the data with contributions from Chris Sutherland, A. Cole Burton, and Solène Marion. Gonçalo Curveira-Santos wrote the manuscript. A. Cole Burton, Jason T. Fisher, Chris Sutherland, Emily J. Herdman, Erin R. Tattersall, Christopher Beirne, and Joanna M. Burgar assisted in data interpretation and provided conceptual input. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Curveira-Santos et al., 2024) are available in Figshare at <https://doi.org/10.6084/m9.figshare.22060985.v1>.

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SUPPORTING INFORMATION

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

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