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Multispecies modelling reveals potential for habitat restoration to re-establish boreal vertebrate community dynamics

Christopher Beirne[1] | Catherine Sun[1] | Erin R. Tattersall[1] | Joanna M. Burgar[1,2] | Jason T. Fisher[2] | A. Cole Burton[1,3]

[1]Department of Forest Resources Management, University of British Columbia, Vancouver, British Columbia, Canada

[2]School of Environmental Studies, University of Victoria, Vancouver, British Columbia, Canada

[3]Biodiversity Research Centre, University of British Columbia, Vancouver, British Columbia, Canada

Correspondence
A. Cole Burton
Email: cole.burton@ubc.ca

Abstract

1. The restoration of habitats degraded by industrial disturbance is essential for achieving conservation objectives in disturbed landscapes. In boreal ecosystems, disturbances from seismic exploration lines and other linear features have adversely affected biodiversity, most notably leading to declines in threatened woodland caribou. Large-scale restoration of disturbed habitats is needed, yet empirical assessments of restoration effectiveness on wildlife communities remain rare.

2. We used 73 camera trap deployments from 2015 to 2019 and joint species distribution models to investigate how habitat use by the larger vertebrate community (>0.2 kg) responded to variation in key seismic line characteristics (line-of-sight, width, density and mounding) following restoration treatments in a landscape disturbed by oil and gas development in northeastern Alberta.

3. The proportion of variation explained by line characteristics was low in comparison to habitat type and season, suggesting short-term responses to restoration treatments were relatively weak. However, we found that lines with characteristics consistent with restored conditions were predicted to support an altered community composition, with reduced use by wolf and coyote, thereby indicating that line restoration will result in reduced contact rates between caribou and these key predators.

4. *Synthesis and applications*. Our analysis provides a framework to assess and predict wildlife community responses to emerging restoration efforts. With the growing importance of habitat restoration for caribou and other vertebrate species, we recommend longer-term monitoring combined with landscape-scale comparisons of different restoration approaches to more fully understand and direct these critical conservation investments. Only by combining rigorous multispecies monitoring with large-scale restoration, will we effectively conserve biodiversity within rapidly changing environments.

KEYWORDS
community ecology, co-occurence, disturbance, human disturbance, monitoring, remote sensing, restoration

1 | INTRODUCTION

Rapid landscape change to meet humanity's growing resource consumption represents a major threat to global biodiversity (Díaz et al., 2019; Maxwell et al., 2016). Reconciling economic development with biodiversity conservation is an urgent imperative requiring bold and effective actions (Doak et al., 2014). While the expansion of protected areas is a critical part of global conservation efforts (e.g. half-earth: Büscher et al., 2017; Wilson, 2016), the need for ambitious conservation and restoration in disturbed landscapes is increasingly highlighted (Kremen & Merenlender, 2018). For example, the global Bonn Challenge seeks to restore 350 million ha of degraded forest landscapes by 2030 (Stanturf et al., 2019). To be effective, such ambitious efforts need to be guided by rigorously assessing socio-ecological responses to restoration.

Traditionally, restoration monitoring has been largely focused on plant recovery (McAlpine et al., 2016); however, it is increasingly apparent that ecosystem-based multi-trophic approaches incorporating interacting community members are vital for effective restoration (Fraser et al., 2015; Ritchie et al., 2012). Frameworks that consider community structure and species interactions in evaluating restoration initiatives are emerging as a critical global endeavour, particularly where restoring wildlife habitats is needed to re-establish species interactions altered by anthropogenic disturbances.

Industrial development to extract natural resources creates substantial disturbances in many of the world's ecosystems (Butt et al., 2013; Venter et al., 2016). For example, petroleum development in the Canadian oil sands region has been linked to altered habitat composition, structure and pollutant levels which led to changes in the composition of terrestrial and freshwater biodiversity (e.g. Fisher & Burton, 2018; Kelly et al., 2009; Mahon et al., 2019). Seismic lines—linear clear-cuts used for petroleum exploration—are ubiquitous in western boreal landscapes (Lee & Boutin, 2006) and contribute to disturbance patterns without historical or natural analogues (Pickell et al., 2015). Seismic lines influence the boreal forest structure in many ways, including altered micro-site topography (e.g. Caners & Lieffers, 2014) and vegetation species composition (e.g.Abib et al., 2019; Van Rensen et al., 2015). Such changes lead to altered habitat use, species interactions and community composition of wildlife (Finnegan, Pigeon, et al., 2018; Pattison et al., 2020). Compounding these impacts, natural regeneration of seismic lines is neither rapid nor ubiquitous (Lee & Boutin, 2006); seismic lines often do not follow typical successional trajectories observed after natural disturbances but rather remain suspended in early successional states (Finnegan, et al., 2018; Finnegan et al., 2019; Van Rensen et al., 2015). The implications of negligible natural regeneration for the boreal ecosystem are profound: alterations in plant species composition and habitat structure, in turn, alter food webs, facilitate the arrival of invasive generalist species (e.g. white-tailed deer—*Odocoileus virginianus*) and put habitat specialists (such as the woodland caribou—*Rangifer tarandus*) at risk (Van Rensen et al., 2015).

Given that natural regeneration is not sufficient to restore seismic lines to their previous state, active restoration efforts have emerged as an important focus for the conservation of caribou and other components of boreal biodiversity (e.g. Bentham & Coupal, 2015; Filicetti et al., 2019). Seismic line restoration initiatives focus on modifying several line characteristics that are assumed to influence both predators and prey, thereby restoring species interactions to pre-disturbance conditions. Reduction in the density of linear features on the landscape through habitat restoration should ultimately support threatened caribou populations through the reduction of predator–prey contact rates (Newton et al., 2017). To date, the majority of studies assessing the potential impacts of seismic line restoration on caribou have been simulation-based (e.g. Serrouya et al., 2020; Spangenberg et al., 2019; Yemshanov et al., 2019), and empirical assessments of restoration effectiveness remain rare (but see Tattersall et al., 2020a).

Empirical assessments of restoration effectiveness are complicated by the fact that altered line characteristics (i.e. vegetation profiles and physical attributes; Finnegan, MacNearney, et al., 2018) have the potential to influence multiple, interacting species in the vertebrate community (e.g. Fisher & Burton, 2018; Heim et al., 2019). Community-level assessments are therefore needed, and an emerging approach for evaluating responses across multiple interacting species is through the use of joint species distribution models (Ovaskainen & Abrego, 2020; Warton et al., 2015). This approach jointly models detections across multiple taxonomic groups while accounting for environmental predictors, allowing the quantification of residual correlations (co-occurrences) between species. Understanding how the vertebrate community responds to habitat restoration, and the potential interactions between species within the community (Aslan et al., 2016), is of key importance if we want to make informed and effective conservation decisions which maximize the benefits of habitat restoration (Burgar et al., 2019; Fraser et al., 2015).

Here, we used camera traps to empirically determine the response of the terrestrial vertebrate community to seismic line characteristics in northeastern Alberta. As the slow rate of vegetation growth in boreal forests precluded longitudinal assessments of restoration effectiveness through time, we used a space-for-time approach which capitalized on recent linear restoration activities that resulted in diverse seismic line characteristics hypothesized to differentially affect species within the community. We examined community-level responses to seismic line restoration using standardized camera trap deployments, controlling for variation in habitat, seasonality, temporal trend and sampling effort. We tested the overarching hypothesis that species within the community show divergent responses to seismic line characteristics, and used model predictions to assess the potential effectiveness of restoration activities at restoring community composition.

2 | MATERIALS AND METHODS

2.1 | Study site

The study was conducted within a 570 km² area of western sedimentary basin boreal forest along the Athabasca River, approximately

70 km southwest of Fort McMurray, Alberta (Figure 1). The site is situated within the Athabasca Oil Sands Region, and is composed of a matrix of lowland terrain (consisting of wet, poorly drained, bogs and fens) and mesic upland sites (primarily along river valleys). The anthropogenic habitat disturbance in the site is principally related to legacy seismic lines, with a moderate seismic line density of 1.1 km/km^2 (below the eastern Alberta average of 1.5 km/km^2; Lee & Boutin, 2006) and an average line width of 5 m.

The initiative to restore legacy seismic lines in the study area (Algar Caribou Habitat Restoration Program) began treating lines in 2012 and was completed in 2015 (Nexen & Silvacom, 2015). The programme's origins, objectives and definitions are described in more detail in Tattersal et al. (2020b). For the purposes of assessing wildlife responses to the restoration programme, we identified line segments according to five experimental categories as sampling strata: (a) 'active restoration' sections prepared by mechanically mounding soil, adding coarse woody material (i.e. dead trees), and planting black spruce seedlings in densities (400–1,200 stems/ha); (b) 'passive restoration' sections where naturally regenerating vegetation (>1.5 m in height and crown cover >50%) was protected from any human disturbance; (c) 'human use' segments were maintained in an open state for human access; (d) 'control' line sections were candidate areas for active restoration set aside as un-manipulated controls; and (d) 'offline' areas were in contiguous forest at least 100 m from a seismic line.

2.2 | Camera trap sampling

We deployed 73 camera stations using a stratified random design, with stations within each of the five strata resulting in sample sizes of 22 active restoration, 12 passive restoration, 14 human use, 12 control and 13 offline. Two stations, including one control and one passive restoration, were converted to human use in April 2018. The average spacing between camera traps was 1.44 km (min = 0.34 km; max = 3.00 km). The number of camera stations increased over time: an initial deployment in November 2015 (24 stations) focused on actively restored and control lines, an expansion of 36 stations in November 2016 to increase actively restored line coverage and extend into human use and passively regenerating lines, and a final expansion in November 2017 (13 stations) to provide an offline control (see Appendix S1 in Supporting Information). Cameras were run continuously at the same location from the date of deployment until November 2019 (aside from times when cameras failed or the viewshed was obscured by snow; Appendix S1). All stations had a single Reconyx PC900 camera trap set at approximately 1 m height at the edge of a line (or wildlife trail for offline stations), perpendicular to the line feature and approximately 3–5 m from the line centre to minimize variation in detection probability across camera stations. Cameras were set to take one photograph with each detection, with no lag time between detections. The species and observed group size of all resultant images were identified by one of four observers (CB, CS, ET and JB), and images of uncertain identity were referred to a fifth observer (ACB) for verification. Raw detection data were aggregated into 'independent detections' by grouping detection events of a given species at a given station that occurred within 30 min of a previous detection (Rovero & Zimmermann, 2016). All species which could be reliably identified to species level were initially included (Appendix S2), with 709 observations of non-identifiable species removed out of 7,821 total observations.

2.3 | Modelling framework

We used a joint species distribution modelling approach implemented in the Bayesian 'Hierarchical Modelling of Species Communities' (HMSC) package v3.0 (Tikhonov et al., 2020) within the R statistical environment. Joint species distribution models relate multivariate response terms (here species counts in a given time interval) to hypothesized predictors through a regression framework while quantifying species co-occurrences through random effects (Tikhonov et al., 2020). We do not interpret the estimated species-level co-occurrences as species interactions (see Blanchet et al., 2020), rather we consider them to represent systematic covariance in station-level counts between species that is not explained by the predictors in the model. The response term in our models was a two-dimensional 'station_time' by species matrix, where each row specified the number of independent detection events within a given 6-month (seasonal) time period for a given station. Any station-time period with less than 30 camera-days of sampling effort (due to camera malfunction) was excluded from the modelling. We assumed that our response variable—the number of independent detection events per 6-month seasonal period—was an index of 'habitat use' by species (following Tattersall et al., 2020). While the index of habitat use does not directly account for imperfect detection (i.e. an animal using the location, but not detected), we took steps to standardize detection probability between cameras (specifically using the same camera trap make and model set at consistent heights (70–100 cm), angles [parallel] and target viewsheds). We also focus interpretation on within-species shifts in habitat use rather than direct comparison of detection rates between species, which would be more influenced by species traits (e.g. home range size, mobility and body size; Devarajan et al., 2020). Crucially, the occupancy modelling framework often proposed to address imperfect detection is also susceptible to bias related to animal movement behaviour in camera trap surveys (Neilson et al., 2018).

Five seismic line characteristics were selected as fixed effects which reflect the structure, regeneration status and spatial configuration of the seismic lines within the study area (Appendix S3). These were (a) line-of-sight (m), which represented the mean observable distance in meters along the line (for seismic strata) or game trail (for off-line stations) in both directions, and quantified using a laser range finder (right-truncated at 500 m—the maximum distance quantifiable with the rangefinder used); (b) vegetation height (m), the average of three representative shrubs/trees measured randomly within 10 m of the camera, (c) line width (m); (d) mounding height (cm), measured
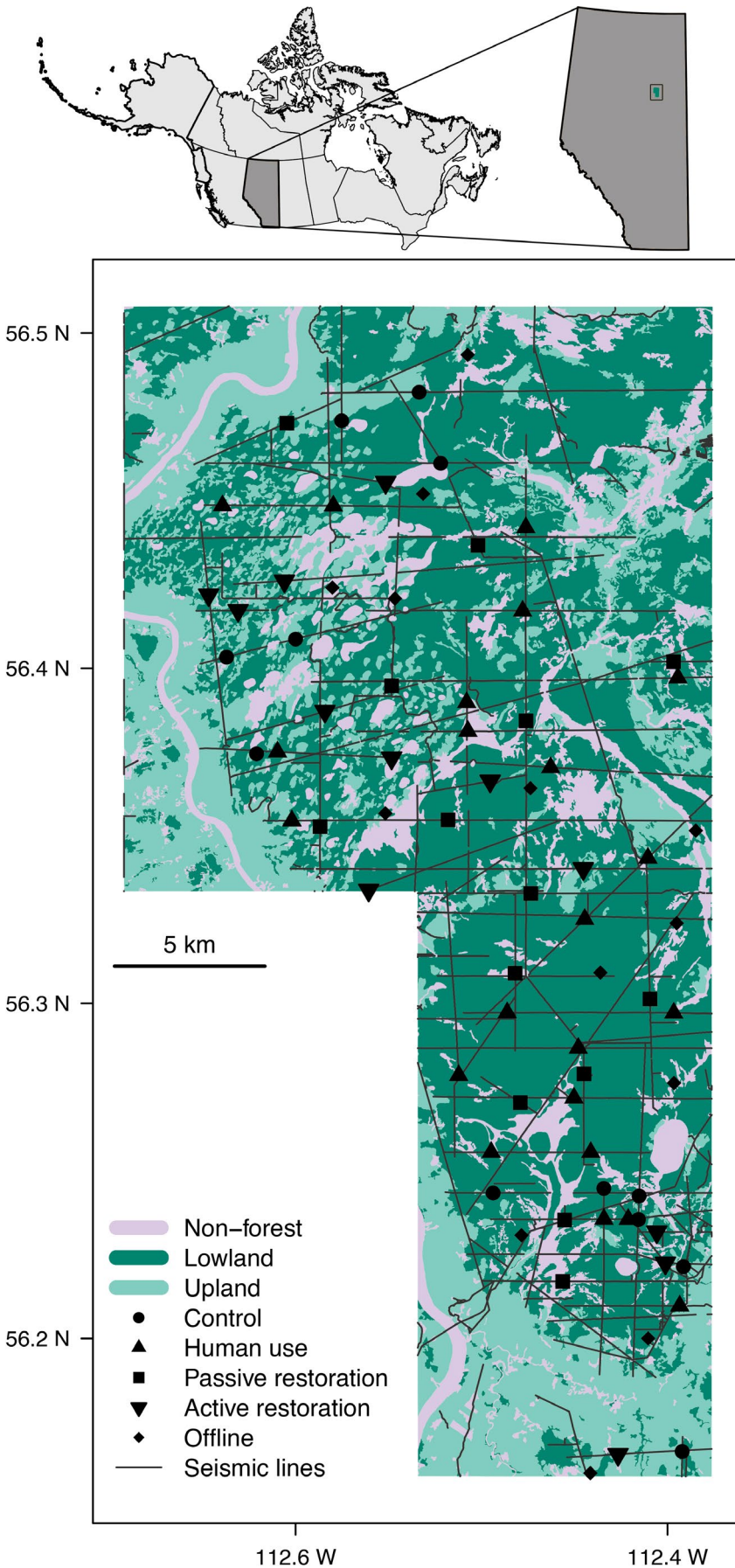
FIGURE 1 Map of the study site context and survey locations. Where: 'Lowland' = forested areas principally comprised of black spruce and tamarack; 'Upland' = mesic forest typically composed of white spruce, aspen and jack pine; 'Non-forest' = non-forested habitats (e.g. rivers, lakes)

at three locations within 10 m of the camera station; and (e) line density (km/km^2) within a 500 m buffer of each camera location was calculated using the Alberta linear feature layer (Alberta Biodiversity Monitoring Institute, unpubl. data). All in situ measurements at camera trap stations were taken in 2017 are thus time invariant. A principal components analysis showed that these continuous predictors adequately discriminated the original strata in multivariate space (Appendix S4). Line characteristics showed low pairwise correlations (correlation coefficients <0.5), except vegetation height was negatively correlated with line-of-sight (−0.68) and line width (−0.53) and was thus excluded from the model (Appendix S5).

In addition to line characteristics, we controlled for a suite of spatial (habitat type and quality) and temporal effects (season, temporal trend and survey effort; Appendix S3). To account for between-station variation in habitat type, we included average distance to water table in the 500 m surrounding each camera location using the 1 m Wet Area Mapping (WAM) layer (White et al., 2012). To control for seasonality in activity patterns, movement behaviour or habitat use, we included a categorical two-level factor distinguishing the two primary seasons: summer (April–September, mostly snow-free) and winter (October–March, mostly snow-covered). We used summer as the reference level. To account for species-specific temporal trends in the count data, including trends potentially due to wolf population management known to occur in the area (Burton et al., 2020), we included a linear effect of survey year (2015–2019). To account for variation in survey effort due to periods of camera trap malfunction, we included the number of days a given camera trap was active in a given time period as a fixed effect (as offsets are not yet supported in the HMSC package: Tikhonov et al., 2020). All predictions shown correspond to the mean days cameras were active in a given 6-month period (156 days). Finally, we included station as a random intercept to account for non-independence of repeated observations from the same station.

We used a Bayesian framework with Markov chain Monte Carlo (MCMC) to estimate the model parameters. Species counts were assumed to follow a Poisson distribution, and species responses to the predictors were assumed to follow a multivariate Gaussian distribution. We used the default, non-informative priors (Tikhonov et al., 2020). Species with 10 or fewer independent detections (Appendix S2) were excluded from the HMSC analysis as their parameter estimates failed to adequately converge. The final model was fit with four MCMC chains, each composed of 2,000,000 iterations with a thinning interval of 2,000 and a burn-in length of 1,500,000, resulting in 1,000 samples per chain. Parameters were confirmed to have converged and mixed well through visual inspection of trace plots, examination of effective sample size and potential scale reduction factor. We used pseudo-R^2 as a measure of model fit, calculated as the squared Spearman correlation between observed and predicted values, times the sign of the correlation (Ovaskainen & Abrego, 2020). We also calculated the proportion of explained variance that was attributable to each of the fixed effects in the model and used this as a measure of relative importance. Species were assigned to co-occurring groups using hierarchical clustering with

Ward's criterion (Ward, 2010) on the residual pairwise correlations between species (after controlling for the fixed effects).

## 2.4 | Predicting the potential for community compositional change

To examine the potential compositional shift of the community in response to variation in seismic line characteristics expected under a full restoration scenario versus a business as usual scenario (no restoration), we used model-estimated parameters to predict species-specific habitat use under 'unrestored' characteristics (i.e. no restoration treatments and no natural regeneration: high line-of-sight = 440 m, high line density = 5.2 km/km^2, large line width = 12 m and no mounding = 0 cm) as compared to under 'restored' characteristics (i.e. expected under full recovery of line characteristics: low line-of-sight = 11 m, low line density = 0 km/km^2, low line width = 0 m and good mounding = 80 cm). We standardized the predictions using estimates for summer and with all other continuous predictors held at their average value. We quantified parameter uncertainty through estimating the 95% credible intervals around the mean of the posterior distribution of predicted habitat use for each species (Ovaskainen & Abrego, 2020).

3 | RESULTS

Total sampling effort was 74,364 camera trap days and resulted in 7,112 independent observations of identifiable vertebrate species (Appendix S2). We removed 6 of the 18 species from the HMSC analysis due to poor convergence (fisher, beaver, otter, wolverine, elk and cougar; data not shown), leaving a species pool of 12. Of these 12, all species showed mean effective sample sizes per chain >600, aside from *Martes americana* (560) and *Vulpes vulpes* (418; Appendix S6). The degree to which the multispecies, joint distribution model explained variation in wildlife habitat use was highly species-specific: comparison of pseudo-R^2 values showed that the model explained over 55% of the variation in habitat use for three species (crane, deer and bear), between 30%–45% of variation for four species (caribou, hare, wolf and moose); and <20% of the variation for five species (coyote, lynx, squirrel, fox and marten; Figure 2).

3.1 | Seismic line characteristics less important than variation in season, habitat and other site effects

Across the vertebrate community, species responses to seismic line characteristics and other modelled factors were highly variable. Taken together, variation in line characteristics (line-of-sight, line width, mounding height and line density) explained less variation in habitat use relative to other predictors (season, habitat type and quality, temporal trend or the station-level random effect),
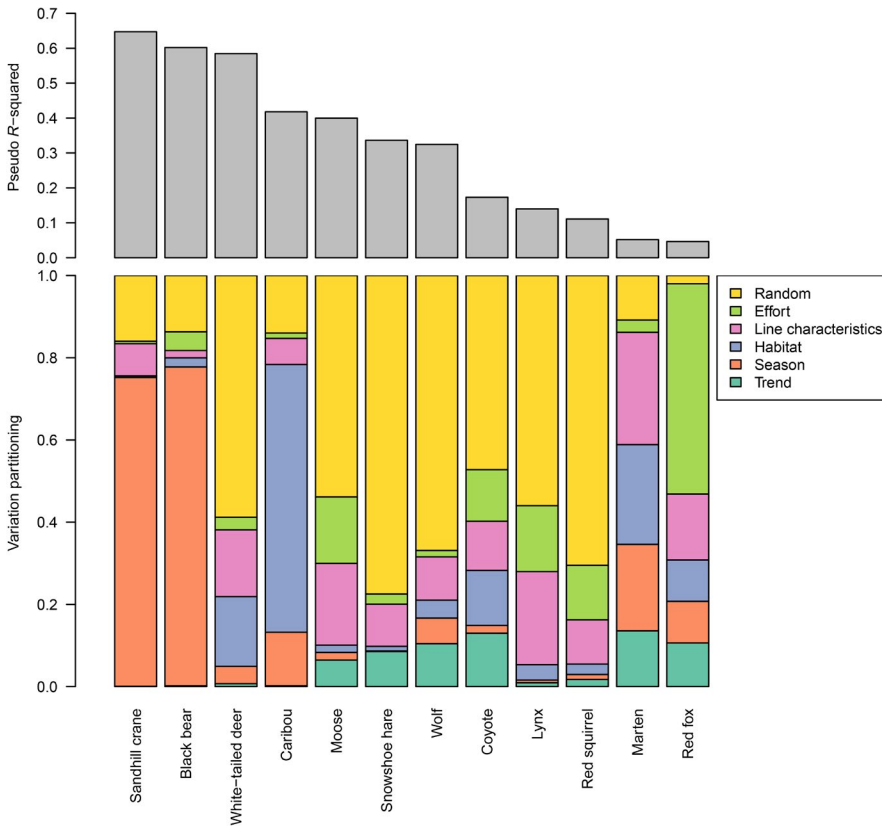
FIGURE 2 Variance explained (pseudo-R^2, top graph) and partitioning of that variance among classes of predictor variables (proportion of explained variance, bottom graph) for each of the species included in the HMSC model. Where: 'Random' represents the variance accounted for by the station-level random effect; 'Effort' represents the variance accounted for by camera deployment length; 'Line characteristics' includes line density, line of sight, line width and mounding height; 'Habitat' represents distance to water table; 'Season' represents summer/winter and 'Trend' represents year. See Appendix S3 for further details
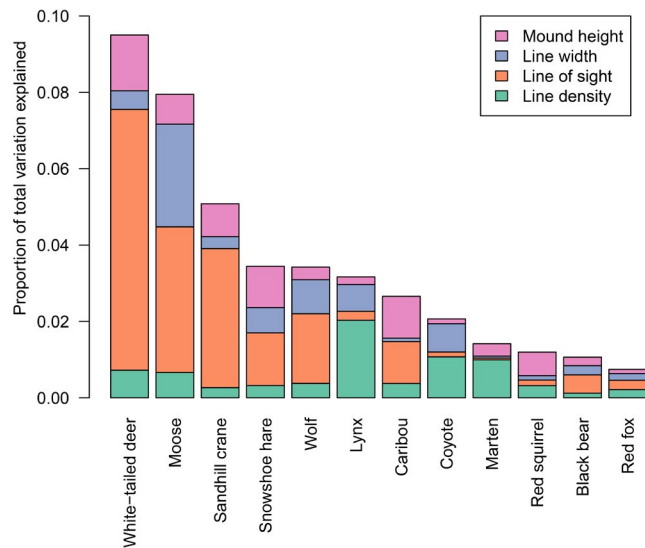
FIGURE 3 The proportion of total variation in species detections explained by the seismic line characteristics

suggesting that line characteristics are relatively weak predictors of line use at the camera station scale (Figure 2).

At the species level, season accounted for the highest proportion of variation explained by the model for hibernating and migratory species (bear = 78% of variance explained by the model, 47% of the total variation; crane = 75% of variance explained by the model, 49% of the total variation), with low relative importance in other species (Figure 2). Habitat variables accounted for the majority of variation

explained by the model for caribou (65% model, 27% total), and a relatively large proportion of variance explained by the model for deer (17% model, 10% total) and coyote (13% model, 2% total). The station-level random effect accounted for the majority of variation explained by the model for seven species (deer, hare, wolf, moose, coyote, lynx and squirrel; Figure 2).

At the community level, the cumulative effect of line characteristics explained no more than 10% of the total variation in habitat use (Figure 3). Decomposing the variation into individual characteristics and averaging the variance explained across all species revealed that line-of-sight explained the highest proportion of variation at the community level (2.0%), followed by line density (0.6%), mound height (0.6%) and line width (0.6%). Line-of-sight explained the greatest proportion of variation in the habitat use of deer (6.8%), followed by moose (3.8%), cranes (3.6%) and wolves (1.8%; Figure 3). Relative to other line characteristics, line density explained the most variation for lynx (2.0%), coyotes (1.1%) and marten (0.9%). Line characteristics had negligible effects on habitat use for black bear, marten, squirrel and fox.

3.2 | Direction and magnitude of responses to seismic line characteristics and other variables

Statistically significant effects of line-of-sight were detected for six species; habitat use was higher with increasing line-of-sight for crane, caribou and wolf, and lower for deer, hare and moose. There was statistical support for a positive correlation between

line density and habitat use for marten, coyote and lynx. Mounding height was positively correlated with habitat use by caribou, sandhill crane, squirrel and snowshoe hare, whereas use by white-tailed deer and marten was negatively correlated. Finally, there was support for greater habitat use on wider lines for coyote, lynx and moose (Figure 4; Appendix S7).

Significant linear temporal trends were detected in 11 species, suggesting changes in habitat use over the study period (Figure 4; Appendix S7). Moose, deer, crane, marten and hare showed significant increases in habitat use through time, while wolf, coyote, fox, bear and squirrel were found to decrease through time. The largest decrease was detected for coyotes.

Consistent with the variance partitioning presented above, factors other than line characteristics and temporal trend had, on average, larger effect sizes across the community. As expected, the habitat use of bear and crane decreased dramatically in winter, as they hibernated or migrated, respectively (Figure 4). Habitat use also declined significantly in winter for caribou, moose, deer, wolf, red fox and coyote, likely reflecting the increased cost of moving in snow or seasonal habitat selection patterns. Only in marten and squirrel did habitat use increase in winter months. Caribou habitat use was greatest at camera stations in closer proximity to the water table, as expected given the affinity of caribou for wetter, lowland habitat

(Figure 4; Appendix S7). Habitat use by coyote, lynx and marten was also higher in wet areas. Deer, fox, wolf and bear were detected less frequently in wet areas.

There were no clear, general patterns in whether habitat use was positively or negatively related to seismic line characteristics across the sampled vertebrate community as a whole, or within the three groups of co-occurring species identified by hierarchical clustering (Figure 4). Group 1 was defined by high co-occurrences among caribou and marten, and to a lesser extent crane. Group 2 showed high co-occurrence between deer, coyote, lynx, hare and squirrel, and negative co-occurrence with Group 1 species. Group 3 contained fox, moose, bear and wolf, which showed no strong patterns with other groups, although bear and wolf tended to co-occur with lynx, coyote and deer (Figure 4).

3.3 | Predicted changes in community structure in response to restoration

The cumulative amount of variation explained by seismic line characteristics appeared to be sufficient to influence predicted habitat use by multiple mammal species (Figure 5). Model-predicted changes in species habitat use suggested the potential for altered
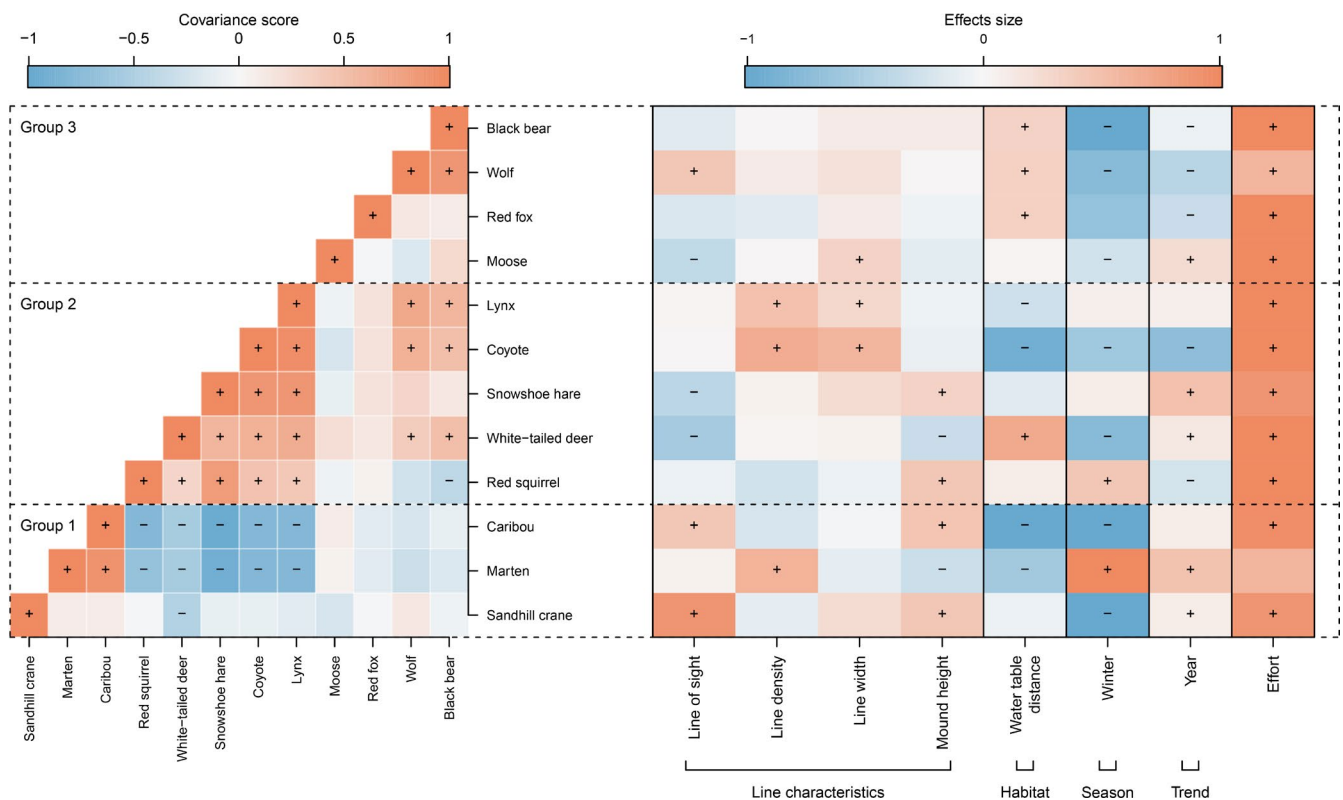
FIGURE 4 Residual co-occurrences between species (left) and estimated effect sizes for the predictors hypothesized to influence habitat use (right) for vertebrates in the sampled community. Values estimated from the HMSC model, and species are ordered and grouped corresponding to the output from hierarchical clustering on residual co-occurrences. Colours denote the estimated covariance between species (left) or standardized effect size (right) and direction; '+' symbols denote positive credible intervals which do not span zero; '−' symbols denote negative credible intervals which do not span zero. For full estimates and confidence intervals, see Appendix S7
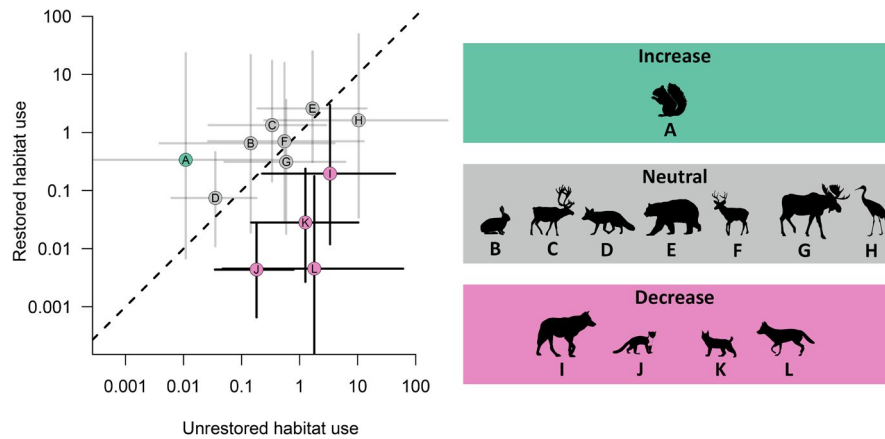
FIGURE 5 Predicted habitat use related to variation in seismic line characteristics in unrestored versus restored conditions. Values on the *x*- and *y*-axes represent the predicted habitat use (posterior means) within an average 6-month sample (163 days). Species which fall: above the dashed line = potential to respond positively to restoration; below the line = potential to respond negatively; and on the line = neutral response; green = species with a mean habitat use change increase of >200%; pink = mean habitat use decrease of >85%; grey = mean habitat use change between; horizontal lines = 95% credible intervals for unrestored habitat use; vertical lines = 95% credible intervals for restored habitat use; black lines = credible intervals which do not overlap the mean estimate of the restoration contrast; A, squirrel; B, hare; C, caribou; D, fox; E, bear; F, deer; G, moose; H, crane; I, wolf; J, marten; K, lynx; and L, coyote

community composition as lines recover from unrestored to restored conditions. The habitat use of wolves, coyotes, marten, and lynx had the most profound predicted decrease under restored conditions, representing decreases in predicted habitat use of 94.1%, 99.7%, 97.5% and 97.7% relative to unrestored, respectively (Figure 5). Restoration of degraded lines was predicted to increase squirrel habitat use by 2,900% (potentially driven by a positive association with mound height), although the wide credible intervals suggested this increase was not significant. The remaining species showed neutral responses to variation in restoration characteristics.

4 | DISCUSSION

The future ecological integrity of western Canadian boreal forests, and of other working landscapes in different ecosystems around the world, depends on our ability to rapidly discover and apply sound ecological rationale to multiple management and restoration decisions. Our research provides a framework utilizing camera traps and joint species distribution models to robustly evaluate terrestrial community-level responses to habitat restoration projects (at least for identifiable species >0.2 kg). We confirm the hypothesis that the direction and magnitude of individual species' responses to seismic line restoration were highly variable across the community as a whole as well as within co-occurring species groups. Encouragingly, our models suggested shifts in community structure in relation to seismic line characteristics, and predicted that restoring seismic lines (i.e. decreasing line-of-sight and line density) may change species' use of linear features, particularly wolves and coyotes. If consistent responses are seen through time and space, habitat restoration can potentially reduce predation risk for caribou over

time, even in the absence of a direct effect of line characteristics on caribou themselves.

The explanatory power of line characteristics was relatively low across all species, which highlights that physical line characteristics are just one of a broad suite of factors (including environmental, climatic, demographic and social elements) influencing habitat use decisions at small (camera viewshed) scales. That said, of the candidate line characteristics, line-of-sight (i.e. impaired visibility due to regrowth) was a significant predictor of habitat use for 50% of species, with the largest average effect size. Restoration initiatives which rapidly and effectively block line-of-sight have the greatest potential to influence predator use. This follows from ecological theory, whereby predation strategies that minimize search times increase predator success (conversely, impeded search and movement decrease success); so decreased wolf use should reduce caribou-predator contact rates (Mckenzie et al., 2012). However, effects of line-of-sight differed among species. Wolves, caribou and cranes all showed reduced occurrence in areas with short line-of-sight. However, caribou habitat use was also positively correlated with line-of-sight (and therefore also vegetation height), potentially reflecting the affinity of caribou for more open lowland habitats. Complete reduction of line-of-sight may not be optimum in all scenarios, especially given that the habitat use of invasive deer (the main apparent competitor for caribou in this system) was higher with decreasing line-of-sight. Consequently, restoration should restore to natural surrounding conditions, rather than 'over restoring' lowland habitat to higher vegetation densities.

Observed community-level co-occurrence patterns are consistent with spatial segregation between caribou, their apparent competitors (deer and moose) and their predators (e.g. Keim et al., 2019; Wasser et al., 2011). Caribou co-occurred less frequently with both deer and their predators (albeit non-significantly), suggesting some

degree of spatial segregation. The key predators of caribou—wolves and bears—co-occurred frequently with each other and with lynx and coyotes. Co-occurrence patterns may be driven by direct species interactions (Tattersall et al., 2020a); however, co-occurrence patterns can also result from other mechanisms (e.g. Blanchet et al., 2020). Therefore, we do not infer direct interactions between co-occurring species in our models, particularly given that the detection frequencies were calculated at the 6-month scale (too coarse for discerning direct interactions), but patterns reflect community composition after controlling for effects of habitat, seasonality and seismic line characteristics.

Seasonality was the strongest predictor of habitat use, unsurprising given large intra-annual fluctuations in boreal temperature and precipitation (e.g. Fisher et al., 2020). Most species had significantly lower habitat use in winter than in summer, particularly the winter hibernating (bear) and migrating (crane) species. Ungulates occurred less frequently in winter, likely mediated by seasonal shifts in home range and/or reductions in movement (and thus habitat use) due to snow and cold (Broadley et al., 2019; Richard et al., 2014). Increased winter habitat use by marten and squirrel potentially reflect an increase in detection probability due to snow cover (increasing their proximity to the camera detection zone or reducing vegetation obstruction). Natural features also predicted habitat use, particularly for caribou and deer which showed opposite relationships to water table depth; species-specific responses to hygric or mesic vegetation likely drives spatial segregation. Caribou exploit wetter, lowland habitat (>60% of variance explained in caribou habitat use); restoration should thus focus on wet sites where natural regeneration occurs slowly or not at all (Van Rensen et al., 2015), although they are the most difficult to restore with slow vegetation recovery rates (Filicetti et al., 2019).

Our 4-year sample facilitated robust assessment of temporal trends in wildlife habitat use, and mitigated spurious inference on environmental drivers of changes in habitat use (e.g. Urbanek et al., 2019). In all, 11 of the 12 species showed evidence of linear trends in habitat use, with six species increasing through time and five decreasing. Four declining species were predators (coyote, wolf, fox and bear—from large to small effect size). Wolf habitat use declines are consistent with active wolf population control in the Algar caribou range (Burton et al., 2020); other predators are harvested under a quota system but not subject to government population control. Corresponding increases over time in habitat use of prey species (caribou, moose, deer, hare and crane), and of a mesocarnivore (marten), are consistent with population or behavioural changes that could be related to a reduction in top-down control due to decreased predator abundance or activity (e.g. Crooks & Soule, 1999).

Although we assessed several of the key structural (e.g. line-of-sight) and spatial (e.g. line density) characteristics of seismic lines expected to affect their use by wildlife, one of the most important predictors of habitat use may be the vegetation characteristics of the site (Finnegan, MacNearney, et al., 2018). The total variation in habitat use explained by our community-level model was low, and the proportion of the total variation explained by station-level random effects was high, particularly for small-bodied consumers (e.g. hare and squirrel) relative to large bodied, focal species (e.g. deer). The low explanatory power in the smaller members of the boreal community (e.g. marten and squirrel) may arise due to small differences in camera microsites (e.g. camera viewshed topography) which cascade into marked station-to-station variation in the detectability of smaller species (Hofmeester et al., 2019). Greater consideration of microsite characteristics through fine-scale camera viewshed metrics or in situ assessments of vegetation composition may make community-level comparisons more robust (Hofmeester et al., 2020; Sun et al., 2021). It is also important to note that although we have used a community-level approach, 6 of 18 species were removed from the analysis due to insufficient detections, and a further two had relatively low estimated sample sizes in the models (fox and marten, for which estimates of uncertainty must be treated with caution). Landscape-scale analyses which synthesize data from multiple projects may be required to generate strong inferences on rarer species.

Multi-species, community-level analysis is an important first step in assessing efficacy of seismic line restoration treatments. We contend seismic line restoration can potentially mitigate inflated predator–caribou contact rates; line-of-sight was the most important factor among the characteristics assessed here. The 'benefits' of seismic restoration to caribou are manifested as reduced predator habitat use, rather than direct effects on caribou themselves. The potential for unintended effects of habitat restoration was uncovered (e.g. predicted declines in use by marten and lynx); thus, the relative costs and benefits of restoration in a given landscape must be evaluated. Future comparisons between different restoration projects are essential to determine if the patterns observed here are generalizable at the regional scale, and future examinations of longitudinal changes at restoration sites will give insight into the rate at which the benefits of habitat restoration will be realized. If ambitious global restoration initiatives, such as the Bonn Challenge, are to help stem global biodiversity declines, we need empirical evidence of the effectiveness of restoration actions on the wildlife communities they support. Failure to achieve restoration goals will compromise our ability to balance economic and ecological objectives on a crowded planet.

CONFLICT OF INTEREST

The authors declare no conflict of interest and note that the project funders had no input on the study conceptualization, design, analysis and interpretation of the data, and no input on the decision to publish these research findings.

AUTHORS' CONTRIBUTIONS

A.C.B. wrote the original funding proposals and developed the camera trap sampling design; J.M.B., A.C.B., C.B. and C.S. managed the field operations, with input from J.T.F.; E.R.T., J.M.B., J.T.F., C.B., C.S. and A.C.B. acquired the data; C.B. analysed data and wrote the manuscript and E.R.T., C.S., J.M.B., A.C.B. and J.T.F. assisted in data interpretation and provided conceptual feedback. All authors provided feedback on drafts of the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.8pk0p2nnz (Beirne et al., 2021).

ORCID

Christopher Beirne https://orcid.org/0000-0003-3988-2031
Catherine Sun https://orcid.org/0000-0001-8650-4012
Erin R. Tattersall https://orcid.org/0000-0003-4644-5294
Joanna M. Burgar https://orcid.org/0000-0003-4724-5286
Jason T. Fisher https://orcid.org/0000-0002-9020-6509
A. Cole Burton https://orcid.org/0000-0002-8799-3847

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