

OIL SANDS MONITORING: MAMMALS
2022-2023 TECHNICAL REPORT



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MARCH 2023



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1. MAIN MESSAGES FOR OIL SANDS MONITORING

The ACME Lab's Oil Sands Monitoring (OSM) Mammal Monitoring Program was funded as requested for 2022-2023. We delivered on field monitoring for four Landscape Units under the BADR design. Here we report the summary statistics from that program, and use a combination of OSM-BADR data and existing data from ongoing research programs in the OSR and beyond, to answer core questions of the OSM program, as well as proposed deliverables in the 2022-23 TBM Workplan, which stem from questions posed last year by the Terrestrial Biological Monitoring's (TBM) Technical Advisory Committee (TAC) and Science and Indigenous Knowledge Integration Committee (SIKIC).

Core Questions

1. *Has the abundance of wildlife species changed?* The answer is yes, as evidenced by all of the papers reviewed in Roberts, et al. ¹ and the papers on white-tailed deer²⁻⁵ and boreal mammal communities⁶⁻¹⁵ we have published in the past. The outcomes of this year's analysis (below) corroborates this finding once again: the abundance of wildlife species has changed, and OS activities are a driver of that change.

2. *To what extent is that change driven by oil sands activities?* That same body of research shows that the effect sizes (the strength of a stressor-response relationship) of some OS features can be greater than roads or forest harvesting, depending on the species examined, and the ecological context considered. Seismic lines are important but so are well sites. This year's analysis delves deeper into those nuances, and highlights that the extent of disturbance within the study landscape, as well as its natural vegetative productivity, affect the stressor-response relationship.

3. *What are the cumulative effects of oil sands pressures on wildlife?* We have asked this question previously by comparing the effect sizes of OS features to combined OS and timber harvesting and transportation features. We have shown that anthropogenic features affect mammal species^{2-4,6,8,9,16} – OS features play a demonstrable role, but are not alone in this. The nuance is around when (and why) OS features have a bigger effect, and this question underpins the analyses we have conducted in 2022-23.

Some ancillary questions have also arisen during TBM TAC discussions and are mirrored from some elements of SIKIC. These center on mammals as indicators:

4. *Why do we monitor all these mammal species rather than a few indicators?* The straight answer is that no mammal species “indicates” any other species. There is no functional redundancy in boreal mammal communities, as there is in more biodiverse southern systems or in other taxa such as plants or perhaps birds. Each species has a unique niche – the set of opportunities and constraints that evolution has allowed the species to exploit its environment. Therefore, each species responds completely differently to OS development; there is no overlap or shared response. Failing to include all species will fail in our goals for OS monitoring.

2022-2023 Questions

Our first question is: *Which single OS or non-OS features most strongly affect each mammal’s relative abundance and distribution?* Here, we use remote camera data collected under the BADR design, in high and low disturbance landscapes, to understand which OS features have the strongest effect on mammal species – and how that effect compares to non-OS features, and the configuration of features of interest. Oil sands features best explained five of the ten species examined; the other species were best explained by forestry and by roads. Both landscape composition and landscape configuration were important in these single-variable models, but for different species. We found cool stuff. A unique landscape feature best explained each species occurrence – a mixture of positive and negative relationships – with mixed support for configuration or composition. These conclusions lend support to the fact that we need to take a cumulative-effects, multi-species approach to OSM mammal monitoring, and there is no one species that can inform all or one feature that is a primary stressor.

Our second question is: *How do mammals’ response to OS activities change with context across the OSR; that is, do species respond negatively to OS activities under some conditions and positively under others?* Building on last year’s analysis, here we examined landscapes across boreal and mountain Alberta to show that for each indicator species, stressor-response relationships – which sit at the core of the TBM conceptual model – change among landscapes, with different contexts. The whole-landscape productivity and magnitude of disturbance change mammals’ response to anthropogenic disturbance at smaller scales. This conclusion emphasizes the importance of monitoring across multiple landscape units identified under the BADR design, implemented across the OSR. It also provides importance guidance to industry and government about where mammals’ response to OS stressors are greatest (and weakest), to allow for adaptive monitoring as well as adaptive management – to target future restoration efforts.

In summary, we show that OS activities are affecting whole mammal communities, that stressor-response relationships vary among landscapes, and that different metrics derived from the same data can each yield unique insights. The BADR design is well positioned to yield valuable information for oil sands monitoring in the coming years.

2. 2022-2023 MAMMAL MONITORING: LANDSCAPE UNIT DATASET SUMMARY

Overview

Mammal monitoring at the scale of landscape units (LUs) followed the OSM Terrestrial Biological Monitoring (TBM)'s Before-After Dose-Response (BADR) design. In 2022-2023 we sampled four LU's identified using the BADR design (Figure 1), spanning high disturbance, low disturbance, pre-disturbance, and mineable LUs. Monitoring at Joint Environmental Monitoring (JEM) sites is reported separately by Alberta Biodiversity Monitoring Institute (ABMI).

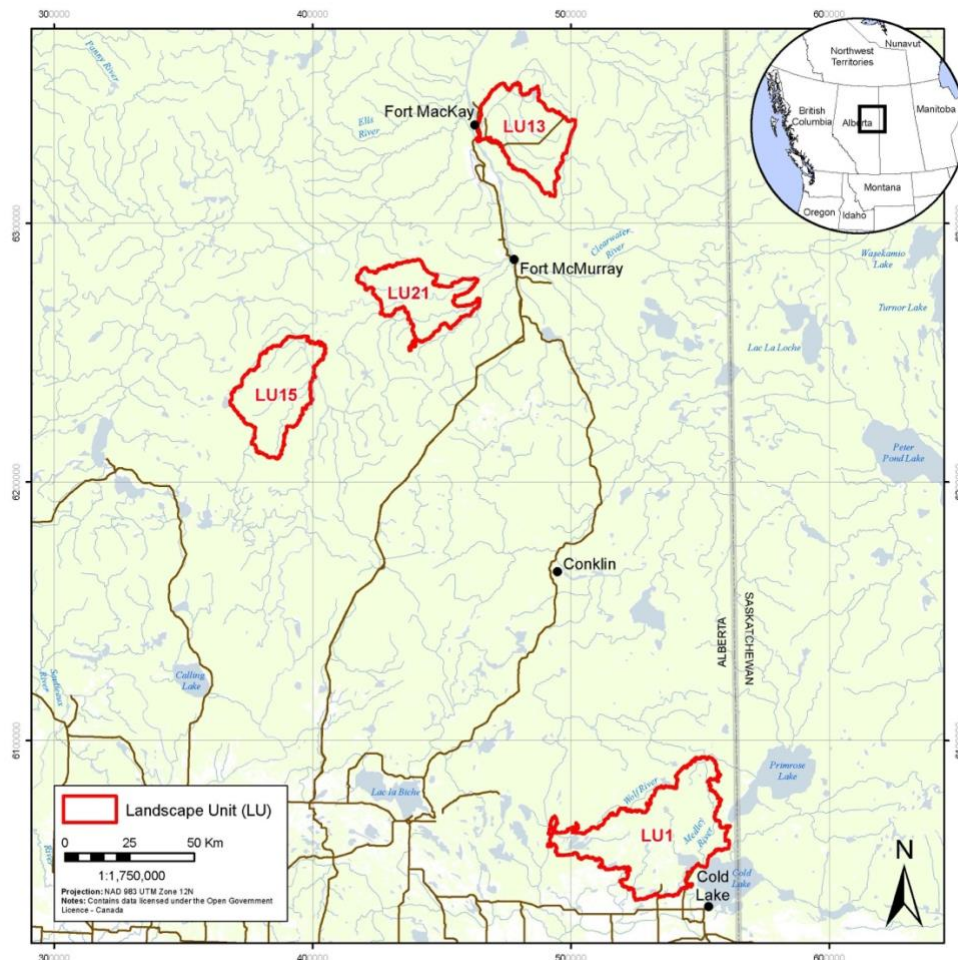


Figure 1. The TBM's BADR design with the four LUs sampled 2022-2023, in the context of the OSR.

Sampling Design

In addition to the JEM sites selected by the TBM team and embedded in each LU, 40 cameras were deployed across each LU in a stratified random design to minimise correlation among environmental covariates and spread sampling effort across the range of natural heterogeneity. The landscape was stratified into dominant (> 50%) forest classes: conifer forest, deciduous forest, and mixedwood forest, using similar criteria as for JEM sites. The intent is to distribute the cameras somewhat evenly among these strata, to “control” for natural variability while examining the role of industrial features on mammal communities.

In ArcGIS the landscape was overlain by a hexagonal grid of 2-km² cells. This cell size allows us to space cameras sufficiently far apart to allow some degree of independence¹⁷⁻¹⁹ for species-habitat models, typically conducted in a linear regression framework^{4,5,15}. It also meets the requirements of density estimation models, which require at least 2-3 cameras be deployed within an individual’s home range size, such that it could be detected on multiple cameras^{14,20-22}. Using data from a review of mammal home ranges sizes²³ and analyses of caribou²⁴ and white-tailed deer²⁵ from the region, we determined the smallest home-range size was for white-tailed deer and that a 2-km² cell size would accommodate model requirements.

Where possible we constrained the resulting hexagonal grid to cells within 100-m of a vehicle-accessible road or trail, as determined by ABMI human footprint inventory. This logistical necessity reduced expensive helicopter time, although in the low-disturbance landscape helicopter access was required for access to all sites. We then randomly selected 30 cells from each of the three strata. When we could not find 30 cells within each stratum, we relaxed the definition of “upland” or “lowland” from > 50% of the cell to > 25% of the cell, and then randomly selected sites to yield a complete set of candidate sites (Figure 2a).

In the field, the deployment team visited each accessible cell and identified active wildlife trails suitable for deployment within that cell (ensuring that cameras within adjacent cells were the minimum 1-km apart); this increases probability of detection given animal presence within the cell²⁶⁻²⁸, as data density is important to make statistical models function¹⁴. No bias is expected²⁹ as game trails represent where wildlife use these complex landscapes; in fact not using game trails biases estimates downward, because one is sampling places that animals do not use, or use very rarely. One Reconyx PC900 or Hyperfire II camera (Holmen, WI, USA) was deployed within the hex cell and secured to a tree using a Reconyx lock box and a

python cable lock. The statistical unit is thus the cell, not the site itself, and the cell is the basis for modelling and inference. At a subset of sites, ABMI deployed an additional camera directly at the cell centroid to represent a random paired site which will allow for improved interoperability of datasets for different density estimation methods^{30,31}. This design was fully integrated with the JEM-site scale sampling. That is, where a JEM site falls within a cell, the JEM site was used – there is no double-sampling. This integrated approach is not only more cost-effective, but it also allows us to conduct cross-scale comparisons key to the hierarchical BADR design. The final deployment spanned major gradients of interest across the LUs (Figure 2).

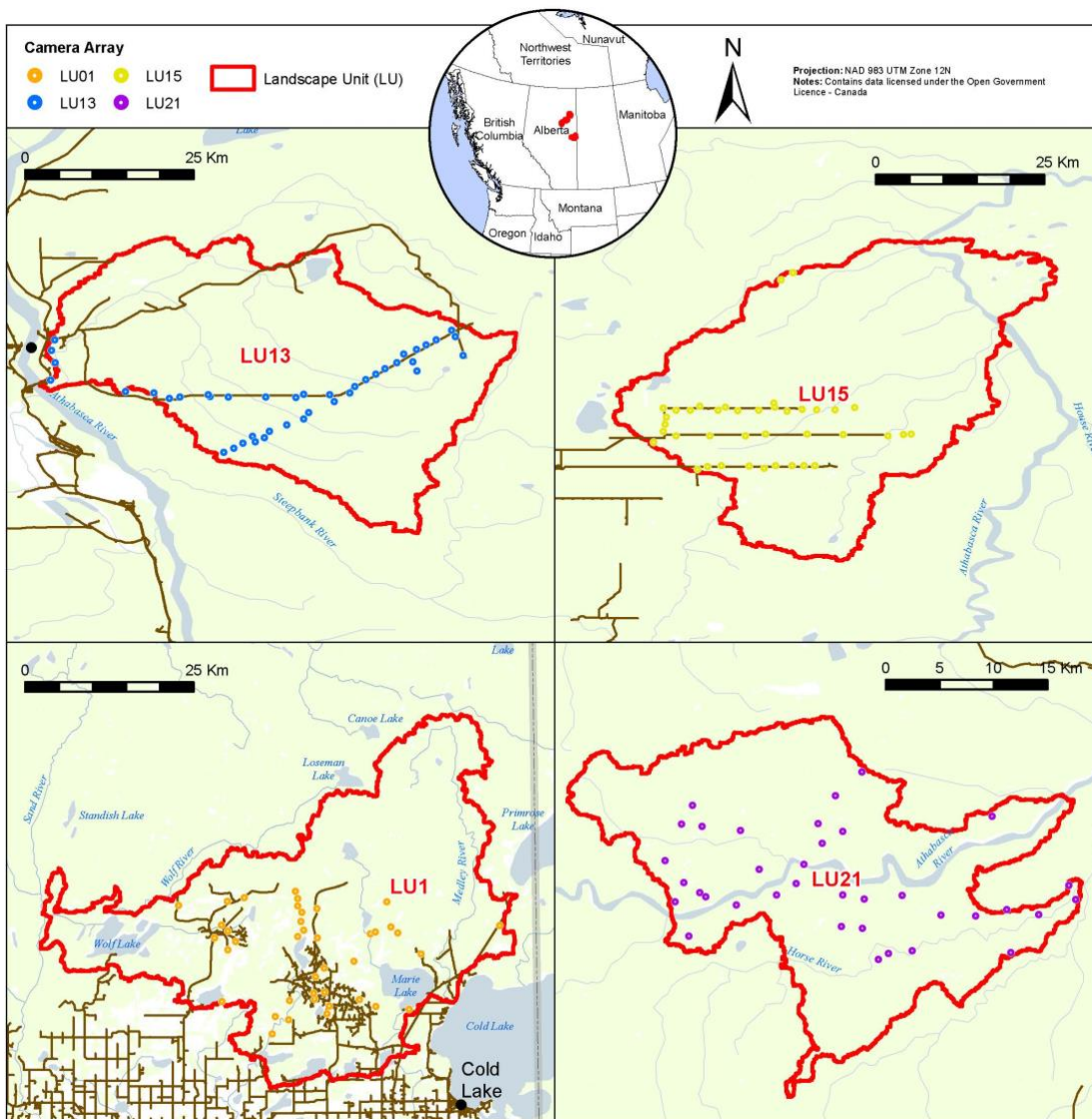


Figure 2. OSM mammal sampling sites in 2022-2023 within the four Landscape Units (LUs).

Monitoring Results to Date

Workplan approvals for the April 1 – March 31 fiscal year were provided April 28, 2022. The AEP research agreement with UVIC was finally signed October 2022. Due to the late approvals and length contract process, deployment occurred September 2022. Based on our analysis of 2021-2022 monitoring results (Figure 3), we decided that a one-year sample is required for most effective LU-scale mammal monitoring. This is consistent with all our past camera-trapping research in the boreal forest^{4-9,11-15,32}. A smaller timeframe reduces detections, especially of rarer species – those of which may be the most susceptible to OS stressors. The complex models we are using to estimate density, stressor-responses, and the mediating effects of species interactions, require large amounts of data equating to variation in detections over time. Therefore we made the decision to collect the cameras in *September 2023*, so image classification of those cameras will occur at that time. In the interim, an updated analysis of 2021-2022 LUs (2 and 3) is presented. The 2021-2022 report contains partial data collection from these LUs as we could not access all sites in the February period need for the March 31st report, so we finalized data collection in June and September of 2022. From here on, we will continue collecting and deploying cameras in the late summer period and obtaining one-year samples.

LU2 Array

Excluding unknowns, 20 different mammal species were detected within the LU2 array. The top four most frequently detected species were White-tailed deer (n = 2330), Snowshoe hare (n = 1251), Black bear (n = 417), and Coyote (n = 76) (Figure 3A). White-tailed deer and Black bears were detected at 100% of sites in the LU2 Array, whereas Snowshoe hare (75%) and Coyotes (68%) were also widespread (Figure 3B).

LU3 Array

Excluding unknowns, 16 different mammal species were detected within the LU3 array. The top four most frequently detected species were White-tailed deer (n = 974), Snowshoe hare (n = 474), Black bear (n = 243), and Coyote (n = 151) (Figure 4A). Black bears and White-tailed deer were the most widespread, detected at 93% of sites; Snowshoe hare, Lynx, and Coyote were close at 78% (Figure 4B).

Relative Abundance

In Figures 5-6, for each array we plot the relative abundance for independent detections of mammal species. Note the substantial differences in species detections among LUs, which is the signal that the Landscape Unit was designed to detect under BADR.

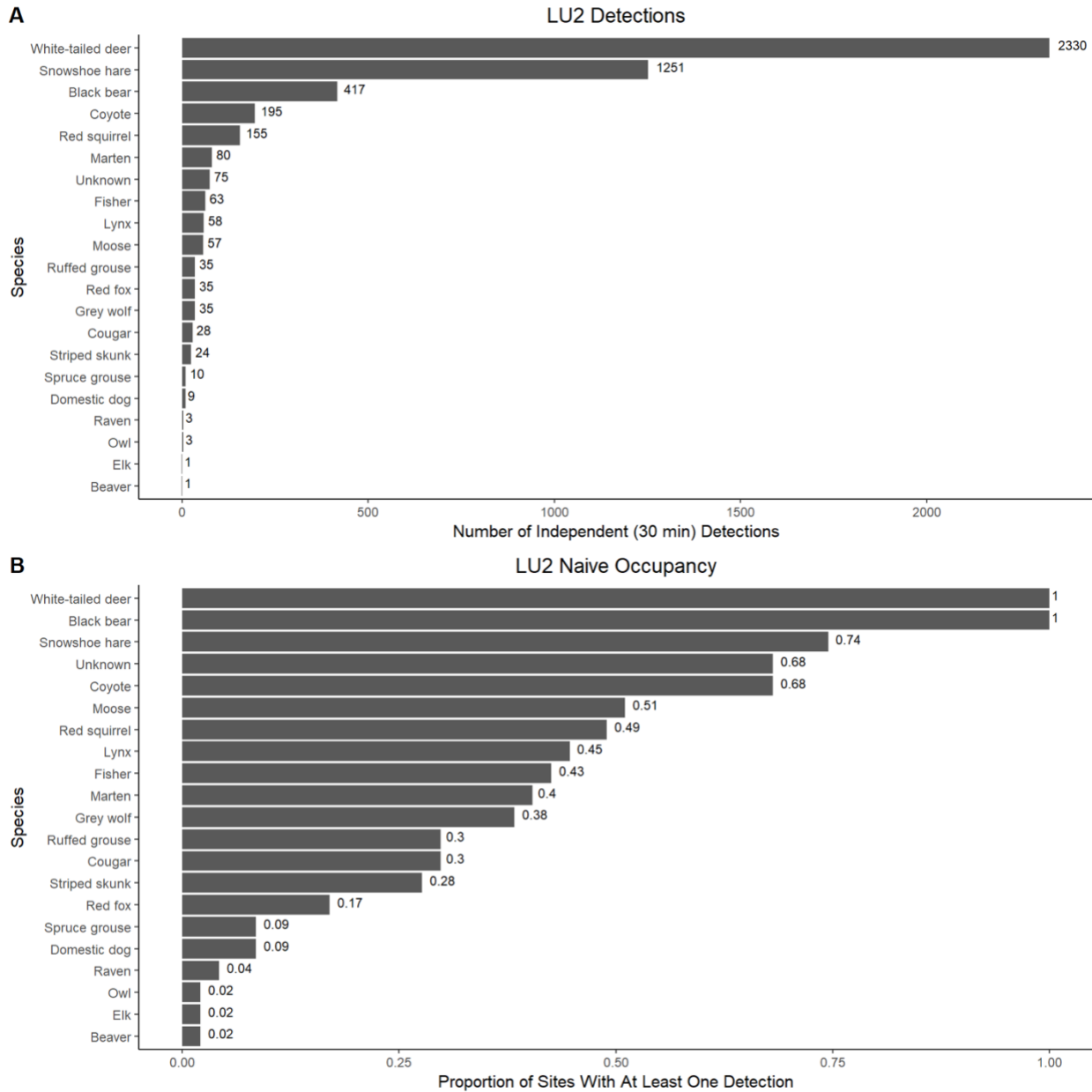


Figure 3. Summary results of A) independent detections and B) naïve occupancy from the LU2 array. Data sourced from 47 cameras: all deployed July 2021, 21 collected in Feb 2022, 26 collected in September 2022.

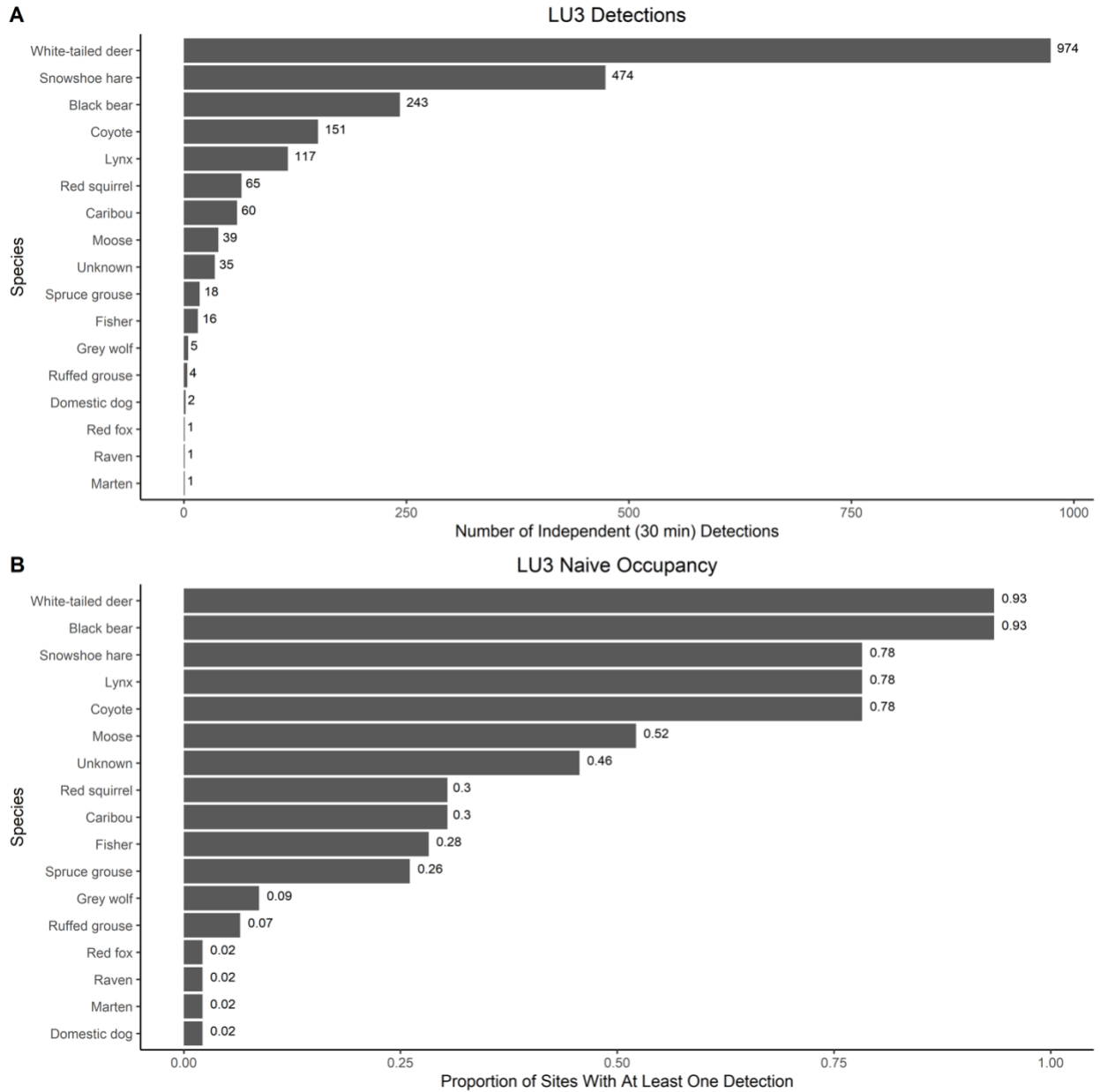


Figure 4. Summary results of A) independent detections and B) naive occupancy from the LU3 array. Data sourced from 46 cameras: all deployed July 2021, 33 collected Feb 2022, 13 collected June 2022 to September 2022.

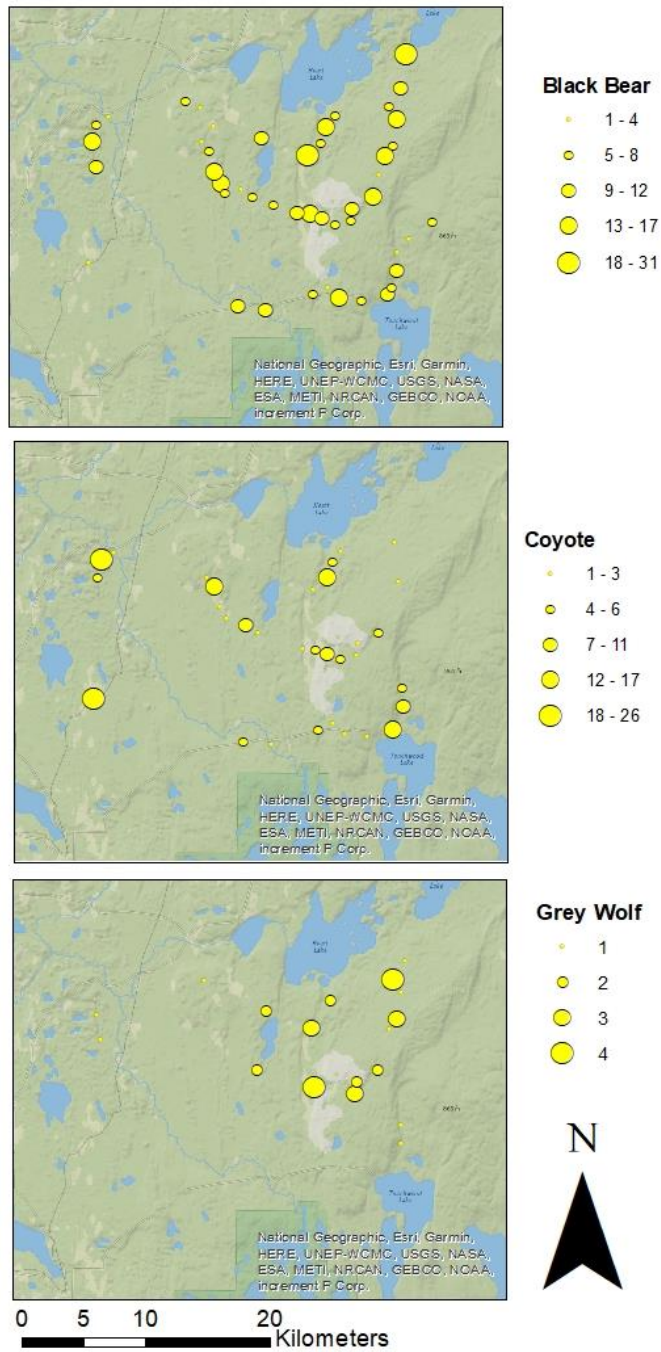


Figure 5A. Relative detection frequencies for black bear, coyote, and grey wolves in LU2.

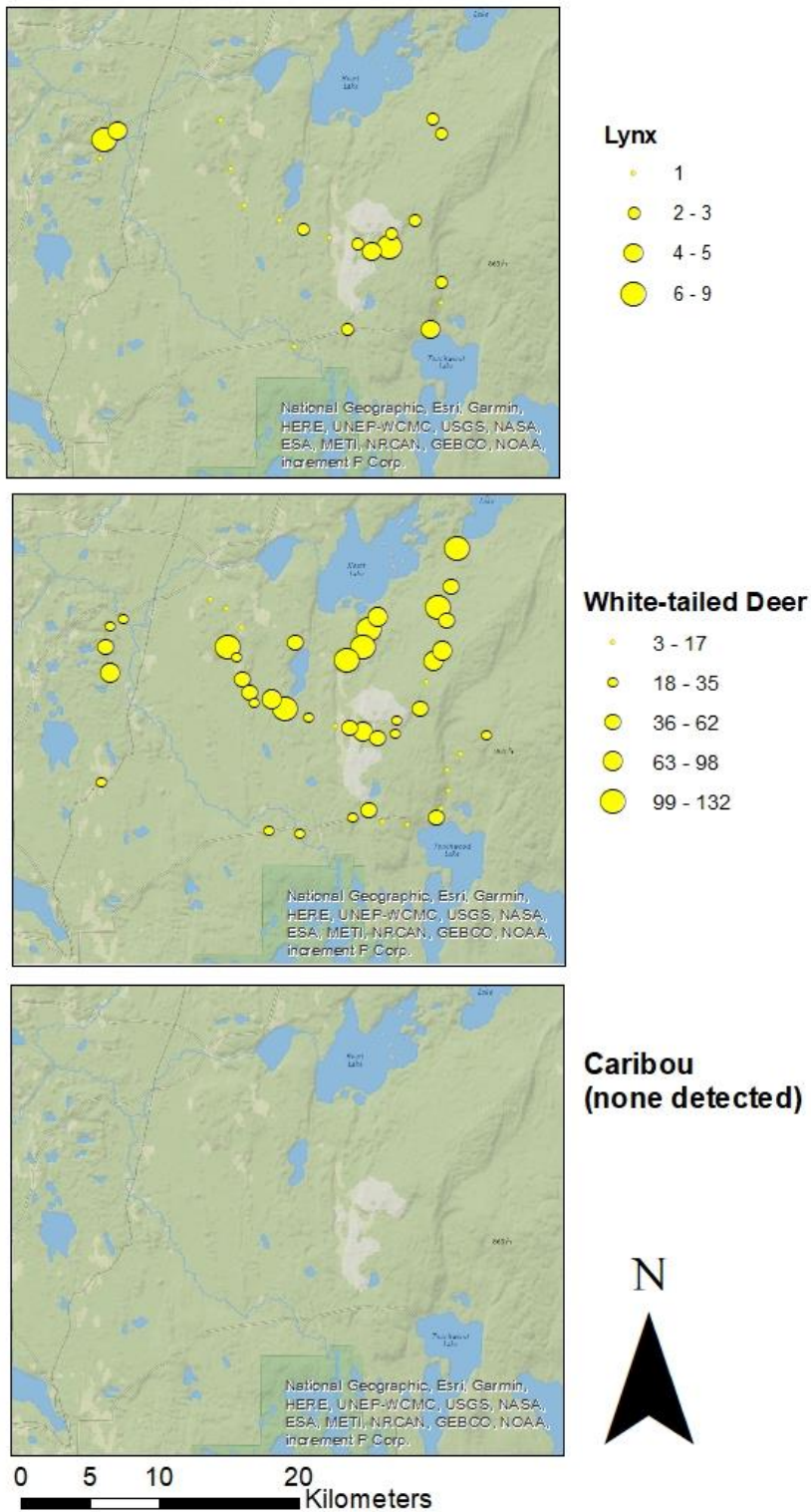


Figure 5B. Relative detection frequencies for lynx, white-tailed deer, and caribou in LU2.

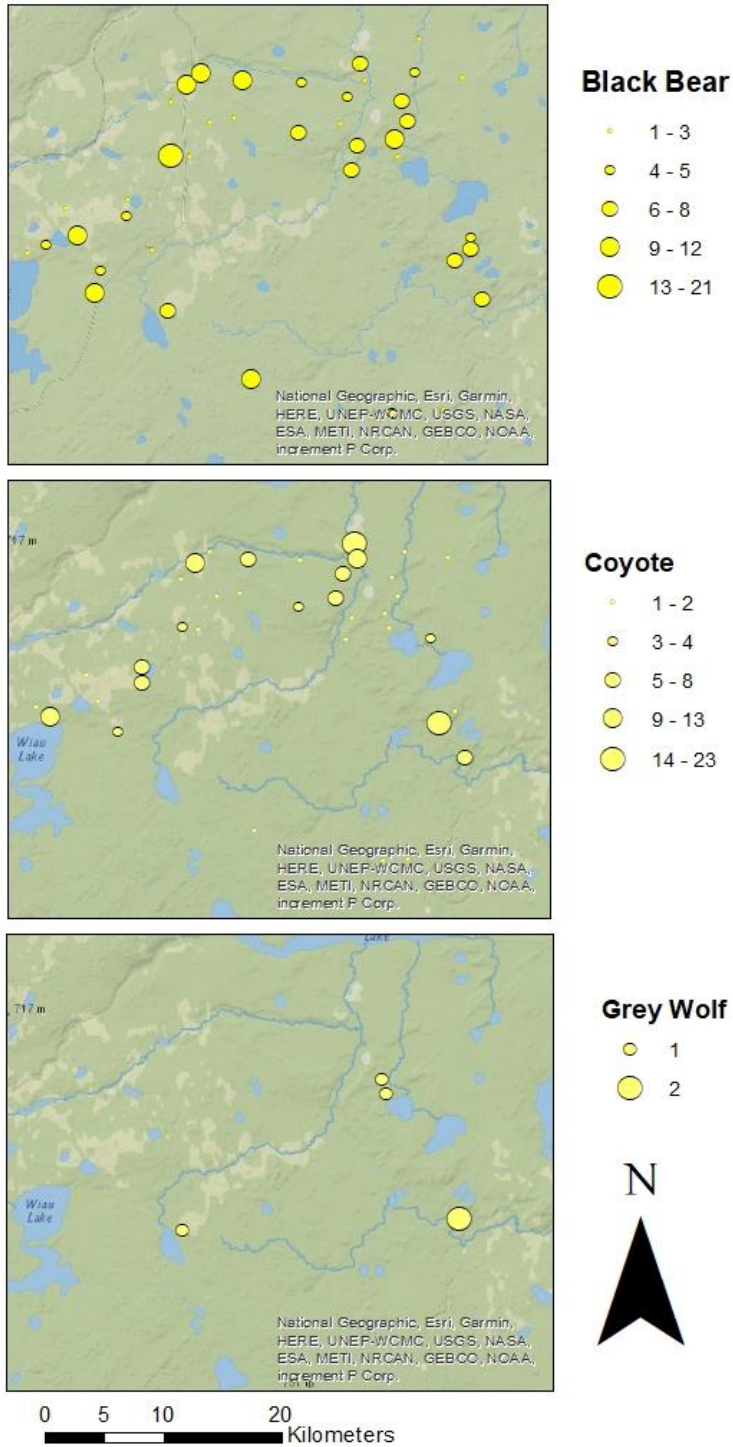


Figure 6A. Relative detection frequencies for black bears, coyote, and grey wolves in in LU3.

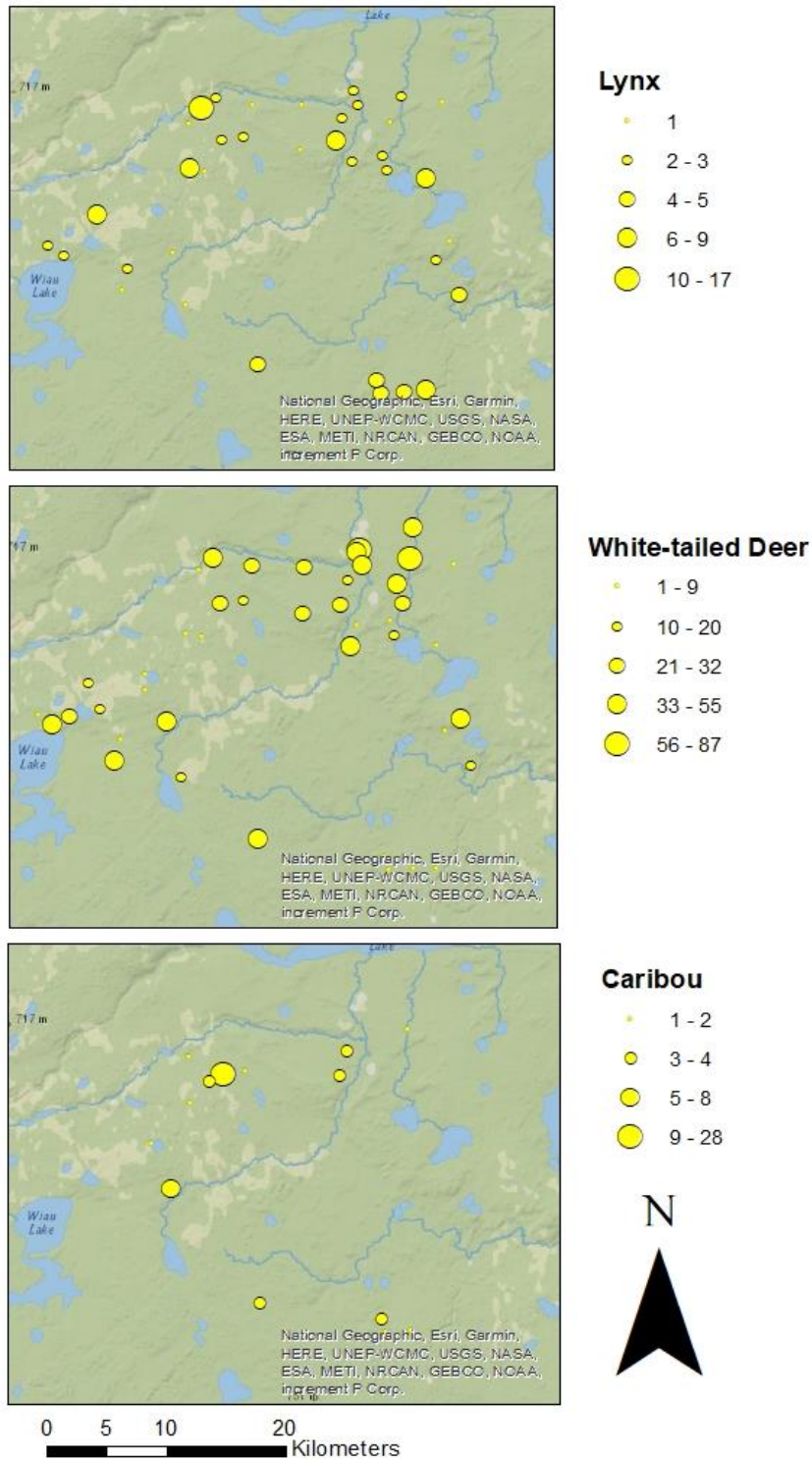


Figure 6B. Relative detection frequencies for lynx, white-tailed deer, and caribou in LU3.

ACME Lab Public Data Portal

The ACME Lab's data portal lists maps and metadata for OSM's TBM Mammal Monitoring Program for 2021 (<http://www.acmelab.ca/osm2021.html>) and 2022 (<http://www.acmelab.ca/osm2022.html>). This portal describes where and when monitoring has occurred. That portal links point to the University of Victoria's data repository: *Borealis Data*. Here, data associated with research is permanently archived with associated DOI's. Each LU is linked as its own project, and each project contains:

1. GIS shapefiles of the deployment sites.
2. Landcover covariates around each camera site, as derived from the ABMI's *Wall-to-Wall Land Cover Inventory* (<https://abmi.ca/home/data-analytics/da-top/da-product-overview/Data-Archive/Land-Cover.html>).
3. Anthropogenic feature covariates around each camera site, as derived from the ABMI's *Wall-to-Wall Human Footprint Inventory* (<https://abmi.ca/home/data-analytics/da-top/da-product-overview/Human-Footprint-Products/HF-inventory.html>).
4. Data extracted from camera images using *TimeLapse Image Analyzer 2.55*³³ in CSV format.
5. Dataframes for R statistical software³⁴ that merge all the associated datasets and provide code for exploring the modelling the data.

3. DO OIL SANDS FEATURES OR OTHER DISTURBANCE FEATURES HAVE THE GREATER EFFECT ON MAMMAL DISTRIBUTION AND ABUNDANCE? THE ROLES OF CONFIGURATION AND COMPOSITION.

OSM Summary

An often-asked question in the TBM TAC meetings is “*How do oil sands features stack up against other anthropogenic features as stressors on biotic indicators?*” Our past research has shown the importance of cumulative effects of multiple stressors – including OS features – on mammalian distribution and abundance. Here, we tackle this question by examining how mammals respond to a *single anthropogenic feature type* by examining responses to a variety of OS and non-OS anthropogenic features. We explore which feature type explains the most variation in mammal relative abundance, measured as the number of months of occurrence of a species at a camera site.

Moreover, we examine the relative role of landscape composition and configuration of these features at multiple spatial scales. Past OSM research on the responses of boreal mammals to OS features have focussed on the *amount* of development around monitoring sites^{1,3-6,8,9,15} – known as landscape composition³⁵. However landscape configuration³⁵ – the shape and juxtaposition of anthropogenic landscape features – can also markedly affect a species’ response to disturbance³⁶. For example, forest-harvest cutblocks are typically large polygons whereas 3D seismic are dense networks of short lines. Patch shape affects *why* a landscape feature is selected (or avoided) by a species. Famously, linear features facilitate wolf travel³⁷ which then increases encounter and predation rates, affecting caribou and moose^{16,38}. Linear features also provide some degree of early seral vegetation resource subsidy that benefit herbivores^{2,3,39-43}. However, polygonal anthropogenic features provide a bigger area of forage subsidy^{15,44,45} and we might expect forest cutblocks to outrank OS features in this regard⁴⁶. However, the small area of OS well sites, offering early seral forage but embedded in a forest matrix that provides escape cover, has an even greater effect for some species^{6,9,15}. Oil sands monitoring under the BADR design is positioned to answer many of these outstanding questions.

The Main Conclusions

We examines responses to anthropogenic features in 10 species. Oil sands features best explained response five species (black bear, caribou, cougar, fisher, and white-tailed deer); the

other five species (coyote, wolves, lynx, moose, and red fox) were best explained by non-oilsands features (i.e. forestry and roads). Both landscape composition and landscape configuration were important in these single-variable models, but for different species.

How can this knowledge be used for OSM?

Attributing mass changes in terrestrial biological indicators in the Oil Sands Region to specific stressors is one of the goals of OSM. Although it is acknowledged that “cumulative effects” are behind these changes, currently “cumulative effects” is not one the management levers available to industry; it is a lever government can pull but only with cooperation of multiple sectors. We identified that OS features were driving changes to distribution and abundance of five mammal species and are contributory to other species. Well sites, seismic lines, and industrial sites are all implicated for different species. We identify restoration of these sites^{10,12,41,43,47-49} as another management lever to mitigate changes to boreal mammal communities. However, because interacting species are part of the proximal cause of change – as in the case of caribou and wolves, coyotes, and moose – and some of these interacting species are affected by forest harvesting, a whole-landscape approach that also addresses forest-harvest area and placement is needed.

Future Directions

This is the first exploration of landscape configuration vs. configuration for large and mid-size boreal mammals in an OSM context. Future research is needed to parse apart in greater detail the contributions of these measures of landscape disturbance to boreal mammal changes. In other words, the importance of “where is disturbance” vs. the “how much disturbance” must be explored to understand how landscape change is altering mammal species. Doing so will inform the specific management levers that government and industry can pull to help conserve boreal mammal populations.

Introduction

The western boreal forest is changing rapidly as resource extraction creates landscapes without global or historical analogs⁵⁰⁻⁵³. Landscape composition – the amount of different landscape features in each area^{10,35,54} – has changed substantially, with more early-seral vegetation patches and a vast dense network of novel linear features. Past research has shown

that mammal species respond to landscape composition resulting from OS activities and cumulative effects of other disturbances in various ways^{1,3-6,8,9,15}. Much of this response is attributed to patch shape. For example, linear features such as seismic lines and roads facilitate wolf travel³⁷ which then increases encounter and predation rates, affecting caribou and moose^{16,38}. Polygonal anthropogenic features such as cutblocks and well sites provide early-seral forage subsidy^{15,44,45} for herbivores, which then attracts carnivores, also altering predator-prey dynamics⁶. Forestry cutblocks have long been known to attract large herbivores⁴⁶, but the role of well sites has only recently been revealed^{3,9}. The value of cutblocks to moose varies markedly depending on their size and shape: large cutblocks with less edge are not selected as much as smaller cutblocks with high edge, as the latter provide that critical juxtaposition of food and escape cover. In fact a recent analysis suggests landscape configuration – the size, shape, and relative position of patches³⁵ – is a stronger determinant of tropical mammalian diversity than just landscape composition⁵⁵. Though often studied in tropical systems, very little boreal research has tackled landscape configuration, and these studies have been on birds⁵⁶⁻⁵⁸ or small mammals⁵⁹, with some exceptions⁶⁰.

We investigated (1) the single-best landscape feature that explained variability of mammal distribution across a gradient of high-low disturbance, and (2) the relative contribution of some landscape configuration measures vs. landscape composition – the simple area of disturbance. We examined ten mammal species of sufficient abundance to allow modelling detected under the BADR design in LU2 and LU3 in 2021-22.

Methods

Study Area and Sampling Design

The data used for these analyses are from LU2 and LU3, as previously detailed in “Monitoring Results to Date” section within 2022-2023 MAMMAL MONITORING.

Quantifying mammal response

Images were reviewed for species as described in previous sections and based on the number of detections in each array we elected to explore analyses for 10 species: black bear, caribou, cougar, coyote, fisher, wolves, lynx, moose, red fox, and white-tailed deer. We summarized species detections as a proportional binomial response variable representing each

species occurrence at each camera monthly, wherein the species was either present (1) or absent (0), for each month the camera was operating, prorated for camera failures (>0.5 month) and winter hibernation (black bear, December-March). We treated non-detections as true ecological signals in our models; thus more “absences” are indicative of lower site value to the species.

Quantifying Landscape Composition and Configuration

We quantified landscape composition (Table 1) from the Alberta Biodiversity Monitoring Institute (ABMI) 2019 Human Footprint Map, a hybrid of digital classification of 30-metre-resolution Landsat satellite images and enhanced using GIS data provided by the Government of Alberta (<https://www.abmi.ca/home.html>). In ArcGIS we drew circular buffers at 10 spatial scales ranging from 250-m to 2500-m radius around each camera site, and measured the proportion of each composition metric within, sensu Fisher, et al. ⁶¹.

We quantified landscape configuration metrics (Table 1) from a raster file that combined land cover data from the 2020 Land Cover of Canada (NRCAN) with anthropogenic feature data from the ABMI 2019 Human Footprint Map. Using the R statistical package⁶² *landscapemetrics*⁶³, we drew circular buffers at 10 spatial scales ranging from 250-m to 2500-m radius around each camera site, and measured the selected configuration metrics within. There are hundreds of metrics included in the *landscapemetrics* package that can improve our understanding of landscape configuration, we selected the following and applied them to seismic lines and forestry: total edge, aggregation index, interspersion and juxtaposition index, and cohesion. Total edge (TE) represents the amount of edge of a feature, defined as 5m from where one feature type is against any other feature or land cover type. The aggregation index (AI) is a percentage value that represents the adjacency of patches from the same feature type (*i.e.* in the raster file, how adjacent are pixels representing for example, forestry). The smaller the AI value, the more dispersed a particular feature type is on the landscape. The interspersion and juxtaposition index (IJI) describes the intermixing of feature types and landcover classes across a landscape and is often referred to the ‘salt and pepper’ metric. If a feature type is only adjacent to one other feature type or landcover class, the index is closer to zero. If a feature type is equally adjacent to all other feature types and land cover classes, the index is closer to 100. The cohesion metric characterises the connectedness of feature types. For simplicity we included these four

metrics (TE, AI, IJI, cohesion) for one OS feature (seismic lines) and a non-OS feature (harvest areas).

We produced exploratory histograms of composition and configuration variables from both arrays to determine if there was enough variation in each proposed variable to model (Figure 1 and 2). Based on a visual inspection of these plots, we elected to remove 1) mines, 2) railways, 3) transmission Lines, 4) cultivation areas, 5) urban and rural residential areas, 6) harvest areas AI, and 7) harvest areas cohesion. As our ultimate objective here is to construct single variable models, we relaxed requirements of correlations between explanatory variables, however examination of correlation plots identified significant correlations between seismic lines and seismic lines TE (Pearson’s $r = 0.91$, $P < 0.0001$), as well as harvest areas and harvest areas TE (Pearson’s $r = 0.93$, $P < 0.0001$). For simplicity we removed seismic lines TE and harvest areas TE from the candidate variable set.

Table 1. Proposed single-variable models explaining mammal species occurrence (2021-22 data) in the OSR.

VARIABLE NAME	INDUSTRY SECTOR	SHAPE	FEATURE TYPES FROM ABMI DATA*
PIPELINES	OS	linear	Pipelines
SEISMIC LINES	OS	linear	Seismic lines
HOLES	OS	polygon	Borrow pits + sump + dugouts
MINES**	OS	polygon	Mine sites
INDUSTRIAL	OS	polygon	Industrial sites
WELLS-ACTIVE	OS	polygon	Active well sites
WELLS-DONE	OS	polygon	Abandoned well sites
ROADS	Non-OS	linear	Roads
RAILWAYS**	Non-OS	linear	Railway lines – hard surface
VERGES	Non-OS	linear	Vegetated surfaces of roads, and railways
TRANSMISSION**	Non-OS	linear	Transmission lines
URBAN**	Non-OS	polygon	Urban and rural residential
CULTIVATION**	Non-OS	polygon	Cultivation
FORESTRY	Non-OS	polygon	Cut blocks

SEISMIC LINES AGGREGATION INDEX	OS	N/A – measured according to configuration metric	Seismic lines (with ai metric from landscapemetrics R package applied)
SEISMIC LINES COHESION	OS	N/A – measured according to configuration metric	Seismic lines (with cohesion metric from landscapemetrics R package applied)
SEISMIC LINES INTERSPERSION AND JUXTAPOSITION INDEX	OS	N/A – measured according to configuration metric	Seismic lines (with iji metric from landscapemetrics R package applied)
FORESTRY INTERSPERSION AND JUXTAPOSITION INDEX	Non-OS	N/A – measured according to configuration metric	Cut blocks (with iji metric from landscapemetrics R package applied)
TOTAL EDGE OF SEISMIC LINES***	OS	N/A – measured according to configuration metric	Seismic lines (with te metric from landscapemetrics R package applied)
TOTAL EDGE OF FORESTRY***	Non-OS	N/A – measured according to configuration metric	Cut blocks (with te metric from landscapemetrics R package applied)

*Descriptions at https://ftp-public.abmi.ca/GISData/HumanFootprint/2019/HFI2019_Metadata_v2.pdf & <https://r-spatialecology.github.io/landscapemetrics/reference/index.html>

**Not included in final single-variable candidate set of models due to lack of representation across landscapes (see data exploration section for details)

*** Not included in final single-variable candidate set of models due to correlation with other included variables (see data exploration section for details)

Statistical Analysis

We analyzed species responses to the remaining explanatory variables in a two-stage approach. First, to identify the best-supported spatial scale for analysis from among the 10 measured scales, we constructed a global generalized linear mixed model containing all of the remaining explanatory variables at each scale from 250-2500m (binomial errors, logit link) We tested for the inclusion of a random effect of Array ID (LU2 or LU3) at the intermediate scale of 1000m using likelihood ratio tests, and found this random effect structure significantly improved model fit for all species except red fox and cougars (Table 2). We compared each candidate spatial scale model using Akaike’s Information Criterion (AIC), and selected the best supported model as the spatial scale to examine single-variable models (Table 3).

Table 2. Likelihood ratio tests examining inclusion of a random effect (Array ID) in global generalized linear mixed models. $P \geq 0.05$ indicate inclusion of a random effect is not supported.

SPECIES	DF	χ^2	P
BLACK BEAR	1	229.1332	9.21E-52
FISHER	1	140.2154	2.39E-32
LYNX	1	219.1453	1.39E-49
WHITE-TAILED DEER	1	341.6105	2.85E-76
GREY WOLF	1	26.25573	2.99E-07
MOOSE	1	165.2364	8.12E-38
RED FOX	1	0.691267	0.405734
CARIBOU	1	21.61358	3.33E-06
COYOTE	1	271.7014	4.83E-61
COUGAR	1	8.78E-09	0.999925

Table 3. Best supported spatial scale for each species.

SPECIES	BEST SUPPORTED SPATIAL SCALE (M RADIUS AROUND CAMERA)
BLACK BEAR	250
FISHER	2500
LYNX	2250
WHITE-TAILED DEER	1750
GREY WOLF	2250
MOOSE	2500
RED FOX	250
CARIBOU	1000
COYOTE	2500
COUGAR	2250

Next, for each species, we constructed a series of single-variable generalized linear mixed models (except for red fox and cougars, for which we constructed generalized linear models based on LRT results). Models were constructed using the remaining fixed effects, using data on each fixed effect collected at the best supported spatial scale for each species as in Table 3. We performed model selection on these single-variable models to identify the most supported OS or non-OS features for predicting species occurrence. In both stages, all continuous variables were scaled (mean = 0, sd = 1) for computational efficiency and to facilitate comparison of coefficient estimates. For each species, we identified the “top” model and made model predictions for probability of species occurrence across the range of that model’s single fixed effect. Models were fit in package *glmmTMB*^{64,65} in R-Studio v4.2.0.

Results

Landscape features and metrics best explaining each species’ distribution

For most species, a clearly best-supported model (where AIC weight approaches 1) emerged from the candidate set (Table 4). The notable exception is black bear; red fox and wolves also had equivocal support, so that some variables did an equally good job at explaining their distribution. For simplicity, we make model predictions from the top supported model, regardless of Akaike weight, but note in these cases other models may be competitive in explaining species occurrence.

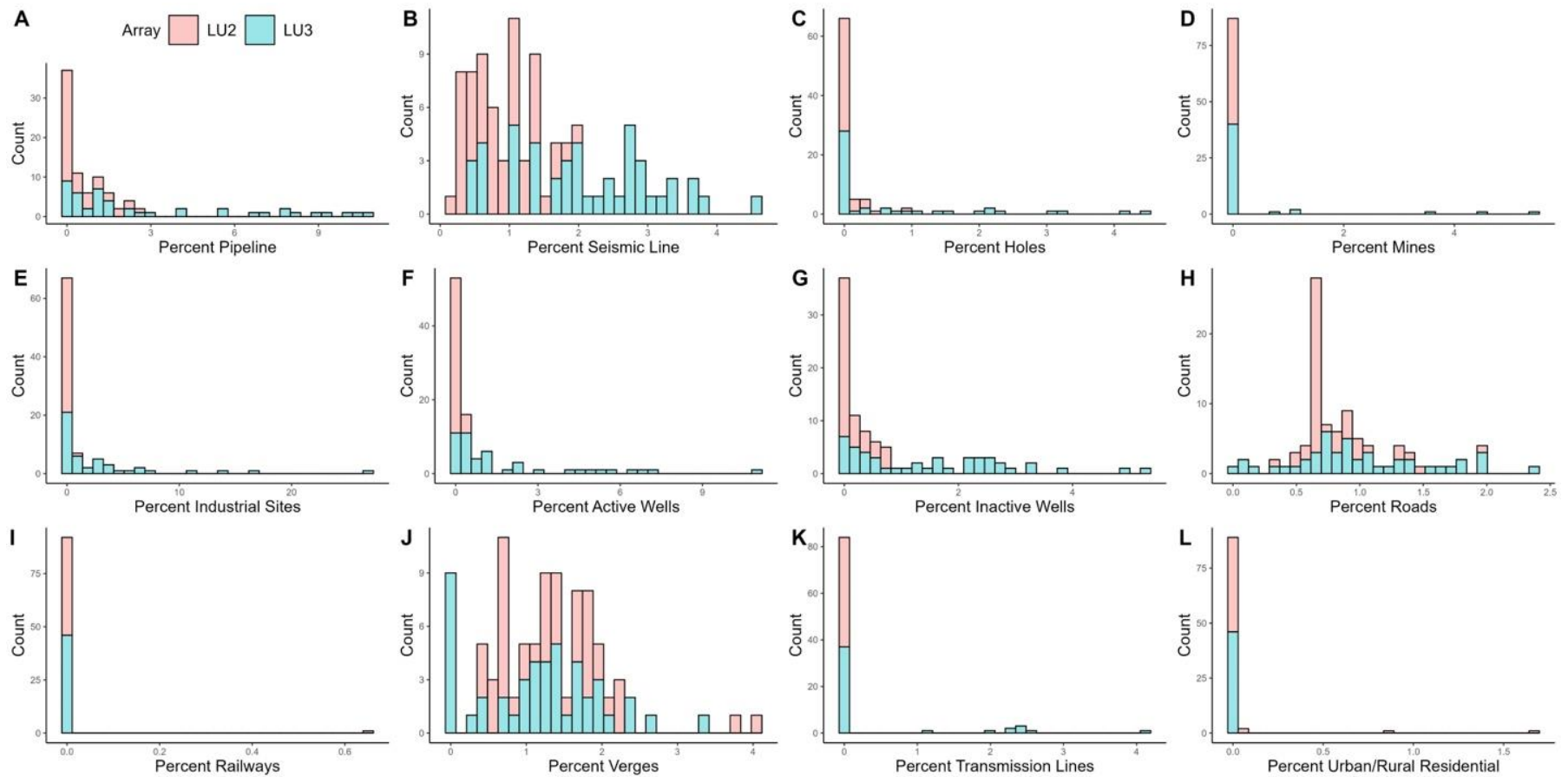


Figure 1. Histograms of proposed model variables (A) pipeline (B) seismic lines (C) holes (D) mines (E) industrial (F) wells-active (G) wells-done (H) roads (I) railways (J) verges (K) transmission (l) urban, measured at the 1000-m radius buffer around camera sites, to explore variable ranges and distributions across LU2 and LU3.

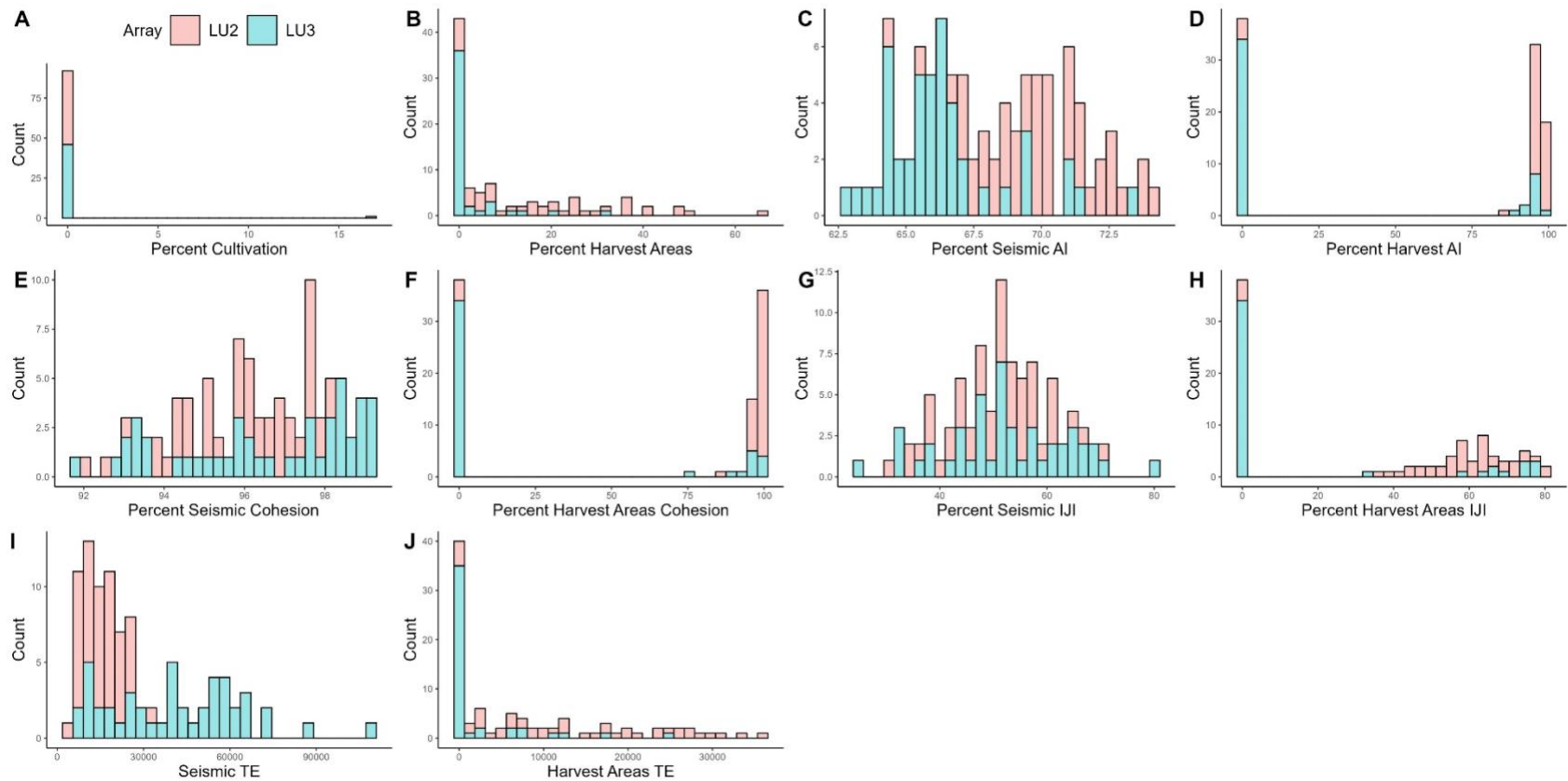


Figure 2. Histograms of proposed model variables (A) cultivation (B) forestry (C) seismic line aggregation index (D) forestry aggregation index (E) seismic line cohesion (F) forestry cohesion (G) seismic lines interspersion and juxtaposition index (H) forestry lines interspersion and juxtaposition index (I) total edge of seismic lines (J) total edge of forestry, measured at the 1000-m radius buffer around camera sites, to explore variable range s and distributions across LU2 and LU3.

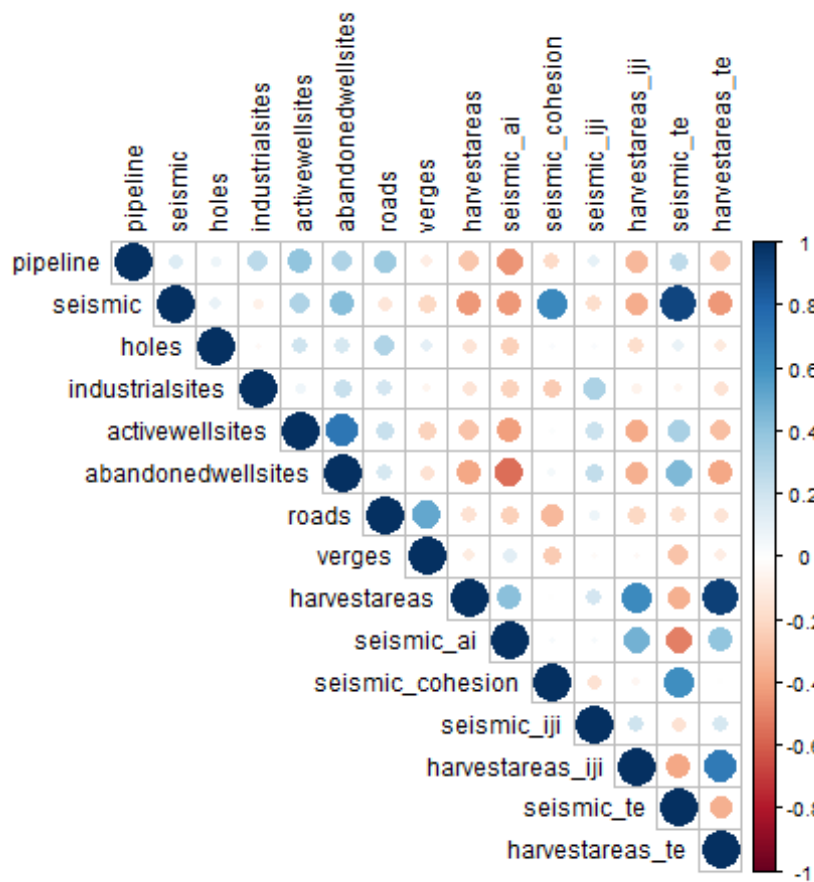


Figure 3. Correlation matrix of all configuration and composition variables proposed in Table 1.

Table 4. The best-supported model for each species. The full candidate sets for each species follow.

ANTHROPOGENIC FEATURE	SPECIES	LOG LIKELIHOOD	AIC_c	AIC WEIGHT
ACTIVWELLSITES	BLACK BEAR	-154.526	315.322	0.122121
SEISMIC	CARIBOU	-51.8455	109.9607	0.74846
ACTIVWELLSITES	COUGAR	-44.6263	93.38598	0.394305
ROADS	COYOTE	-183.603	373.4752	0.661356
SEISMIC_AI	FISHER	-110.673	227.6154	0.886877
HARVESTAREAS	WOLF	-57.1659	120.6015	0.40343
HARVESTAREAS	LYNX	-148.378	303.0261	0.991095
HARVESTAREAS_IJI	MOOSE	-122.719	251.7071	0.704713
HARVESTAREAS_IJI	RED FOX	-49.9852	104.1037	0.317531
INDUSTRIALSITES	WHITETAIL DEER	-226.989	460.2481	0.999777

Black bears

MODEL	LOG LIKELIHOOD	AIC	ΔAIC_c	AIC WEIGHT
ACTIVEWELLSITES	-154.526	315.322	0	0.122121
SEISMIC	-154.756	315.7811	0.459101	0.097073
VERGES	-154.78	315.8303	0.508281	0.094715
ABANDONDEDWELLSITES	-154.867	316.0041	0.682026	0.086834
PIPELINE	-154.91	316.0904	0.76834	0.083166
HARVESTAREAS	-154.913	316.0964	0.774338	0.082917
SEISMIC_IJI	-154.97	316.2097	0.887655	0.07835
HOLES	-155.177	316.6235	1.301483	0.063705
SEISMIC_AI	-155.191	316.6516	1.329587	0.062817
ROADS	-155.235	316.7394	1.417369	0.060119
SEISMIC_COHESION	-155.237	316.7428	1.42079	0.060016
INDUSTRIALSITES	-155.339	316.9472	1.625215	0.054185
HARVESTAREAS_IJI	-155.343	316.9548	1.632749	0.053981

Caribou

MODEL	LOG LIKELIHOOD	AIC	ΔAIC_c	AIC WEIGHT
SEISMIC	-51.8455	109.9607	0	0.74846
ACTIVEWELLSITES	-53.7442	113.7581	3.797316	0.112097
ABANDONDEDWELLSITES	-54.6465	115.5627	5.601966	0.045469
SEISMIC_COHESION	-54.9233	116.1162	6.155427	0.034477
HARVESTAREAS	-55.3201	116.9099	6.949167	0.023183
SEISMIC_AI	-55.3464	116.9625	7.001767	0.022582
INDUSTRIALSITES	-56.3587	118.9871	9.026385	0.008206

PIPELINE	-57.627	121.5238	11.56302	0.002308
HOLES	-58.3239	122.9174	12.95664	0.00115
SEISMIC_IJI	-59.0112	124.2922	14.33142	0.000578
HARVESTAREAS_IJI	-59.0542	124.378	14.4173	0.000554
VERGES	-59.11	124.4897	14.52893	0.000524
ROADS	-59.351	124.9717	15.01098	0.000412

Cougar

MODEL	LOG LIKELIHOOD	AIC	ΔAIC_c	AIC WEIGHT
ACTIVEWELLSITES	-44.6263	93.38598	0	0.394305
INDUSTRIALSITES	-44.9701	94.07349	0.687508	0.279603
ABANDONDEDWELLSITES	-45.3109	94.75517	1.369183	0.198847
HARVESTAREAS	-46.3275	96.78842	3.402433	0.071946
SEISMIC	-47.6213	99.37589	5.989907	0.019731
SEISMIC_AI	-48.3163	100.7659	7.379943	0.009847
PIPELINE	-48.3278	100.7889	7.402917	0.009734
HOLES	-48.5105	101.1543	7.768274	0.008109
SEISMIC_IJI	-48.6445	101.4223	8.036352	0.007092
ROADS	-51.2236	106.5805	13.1945	0.000538
HARVESTAREAS_IJI	-52.1679	108.4691	15.08314	0.000209
VERGES	-54.2526	112.6385	19.25252	2.60E-05
SEISMIC_COHESION	-54.9476	114.0285	20.64255	1.30E-05

Coyote

MODEL	LOG LIKELIHOOD	AIC	ΔAIC_c	AIC WEIGHT
ROADS	-183.603	373.4752	0	0.661356
SEISMIC_IJI	-184.358	374.9864	1.511133	0.310668
VERGES	-187.286	380.842	7.36677	0.016625
SEISMIC_COHESION	-188.472	383.2133	9.73812	0.00508
INDUSTRIALSITES	-189.176	384.6226	11.14742	0.002511
ABANDONDEDWELLSITES	-189.32	384.9088	11.43358	0.002176
HOLES	-190.499	387.2673	13.79209	0.000669
ACTIVIEWELLSITES	-190.688	387.6456	14.17037	0.000554
PIPELINE	-192.537	391.3438	17.86856	8.72E-05
HARVESTAREAS_IJI	-192.646	391.5611	18.08586	7.82E-05
HARVESTAREAS	-192.752	391.7746	18.29937	7.03E-05
SEISMIC_AI	-192.863	391.9954	18.52018	6.29E-05
SEISMIC	-192.867	392.0043	18.52912	6.26E-05

Fisher

MODEL	LOG LIKELIHOOD	AIC	ΔAIC_c	AIC WEIGHT
SEISMIC_AI	-110.673	227.6154	0	0.886877
VERGES	-113.101	232.4726	4.857207	0.078187
ROADS	-115.165	236.5995	8.984089	0.009931
HOLES	-115.453	237.1765	9.561091	0.007442
SEISMIC	-115.751	237.7711	10.15573	0.005528
INDUSTRIALSITES	-116.444	239.1585	11.54305	0.002763
ABANDONDEDWELLSITES	-117.067	240.4042	12.78876	0.001482

ACTIVWELLSITES	-117.072	240.4135	12.79807	0.001475
SEISMIC_COHESION	-117.079	240.4275	12.81204	0.001465
HARVESTAREAS_IJI	-117.174	240.6171	13.00167	0.001332
PIPELINE	-117.274	240.8167	13.2013	0.001206
SEISMIC_IJI	-117.3	240.8706	13.25521	0.001174
HARVESTAREAS	-117.331	240.931	13.31561	0.001139

Wolf

MODEL	LOG LIKELIHOOD	AIC	ΔAIC_c	AIC WEIGHT
HARVESTAREAS	-57.1659	120.6015	0	0.40343
ABANDONDEDWELLSITES	-57.5775	121.4246	0.823053	0.267328
SEISMIC	-57.6133	121.4963	0.894771	0.257912
ACTIVWELLSITES	-59.9039	126.0775	5.475934	0.026103
PIPELINE	-60.9369	128.1434	7.541891	0.009291
VERGES	-61.212	128.6937	8.092205	0.007056
HARVESTAREAS_IJI	-61.2428	128.7553	8.153793	0.006842
SEISMIC_AI	-61.7742	129.8181	9.216534	0.004022
ROADS	-61.8738	130.0172	9.415699	0.003641
SEISMIC_IJI	-61.8747	130.0191	9.417591	0.003637
SEISMIC_COHESION	-61.8852	130.0401	9.438624	0.003599
INDUSTRIALSITES	-61.8906	130.0508	9.449264	0.00358
HOLES	-61.8964	130.0625	9.46102	0.003559

Lynx

MODEL	LOG LIKELIHOOD	AIC	ΔAIC_c	AIC WEIGHT
HARVESTAREAS	-148.378	303.0261	0	0.991095
VERGES	-153.905	314.0803	11.05421	0.003942
ACTIVWELLSITES	-155.471	317.2113	14.18523	0.000824
HARVESTAREAS_IJI	-155.742	317.7537	14.72764	0.000628
ABANDONDEDWELLSITES	-155.889	318.0477	15.02161	0.000542
SEISMIC_AI	-155.934	318.1371	15.11099	0.000519
ROADS	-156.087	318.4427	15.41663	0.000445
PIPELINE	-156.16	318.5889	15.56281	0.000414
SEISMIC_COHESION	-156.205	318.6797	15.65361	0.000395
HOLES	-156.372	319.0141	15.988	0.000334
SEISMIC_IJI	-156.503	319.2765	16.25038	0.000293
INDUSTRIALSITES	-156.514	319.2982	16.27215	0.00029
SEISMIC	-156.559	319.387	16.36091	0.000278

Moose

MODEL	LOG LIKELIHOOD	AIC	ΔAIC_c	AIC WEIGHT
HARVESTAREAS_IJI	-122.719	251.7071	0	0.704713
SEISMIC_AI	-125.618	257.5049	5.797765	0.038819
SEISMIC_COHESION	-125.764	257.7969	6.08977	0.033546
ACTIVWELLSITES	-125.849	257.9685	6.26144	0.030786
SEISMIC_IJI	-125.854	257.9783	6.271187	0.030637
ABANDONDEDWELLSITES	-125.975	258.2206	6.5135	0.027141
INDUSTRIALSITES	-126.089	258.4469	6.73984	0.024237
PIPELINE	-126.108	258.485	6.777905	0.02378

HOLES	-126.241	258.7527	7.045548	0.020801
VERGES	-126.267	258.8028	7.095723	0.020286
ROADS	-126.533	259.3361	7.629004	0.015538
SEISMIC	-126.578	259.4254	7.718266	0.01486
HARVESTAREAS	-126.578	259.4258	7.718715	0.014856

Red fox

MODEL	LOG LIKELIHOOD	AIC	ΔAIC_c	AIC WEIGHT
HARVESTAREAS_IJI	-49.9852	104.1037	0	0.317531
SEISMIC_AI	-50.2112	104.5557	0.451967	0.253304
ABANDONDEDWELLSITES	-50.7198	105.5729	1.469193	0.152319
SEISMIC	-51.5426	107.2184	3.114708	0.066901
HARVESTAREAS	-51.817	107.7672	3.663509	0.050847
SEISMIC_COHESION	-52.3789	108.8911	4.787324	0.028989
VERGES	-52.5665	109.2663	5.162568	0.02403
SEISMIC_IJI	-52.5749	109.2832	5.179488	0.023827
HOLES	-52.7601	109.6535	5.549799	0.0198
PIPELINE	-52.9403	110.014	5.910232	0.016535
INDUSTRIALSITES	-52.9749	110.0831	5.979368	0.015973
ACTIVIEWELLSITES	-52.9994	110.132	6.028313	0.015587
ROADS	-53.0815	110.2963	6.192592	0.014358

White-tailed deer

MODEL	LOG LIKELIHOOD	AIC	ΔAIC_c	AIC WEIGHT
INDUSTRIALSITES	-226.989	460.2481	0	0.999777
ACTIVWELLSITES	-235.504	477.277	17.02895	0.0002
SEISMIC	-237.807	481.883	21.6349	2.00E-05
SEISMIC_COHESION	-240.234	486.7381	26.49008	1.77E-06
ROADS	-241.06	488.3898	28.14177	7.74E-07
HOLES	-245.152	496.5743	36.32627	1.29E-08
PIPELINE	-245.627	497.5237	37.27568	8.05E-09
ABANDONEDWELLSITES	-248.338	502.9466	42.69851	5.35E-10
VERGES	-249.934	506.1373	45.88921	1.08E-10
SEISMIC_AI	-250.193	506.6564	46.40834	8.36E-11
SEISMIC_IJI	-250.524	507.3174	47.06931	6.01E-11
HARVESTAREAS	-251.778	509.8257	49.57766	1.71E-11
HARVESTAREAS_IJI	-251.814	509.898	49.64993	1.65E-11

Model Predictions

Model predictions from the top model for each species show the predicted relationship between the single variable and the probability of monthly occurrence (Figure 4). We identified positive relationships between explanatory variables and occurrence for caribou, coyote, fisher, wolves, moose, red fox, and white-tailed deer. Negative trends were observed for black bear and lynx. We caution interpretation of the results for black bear (Figure 4A) due to the large number of competitive models, and cougars (Figure 4C) due to the restricted range of active-well sites. Further, interpretation of results at the extremes of most variables are notably accompanied by large 95% confidence intervals.

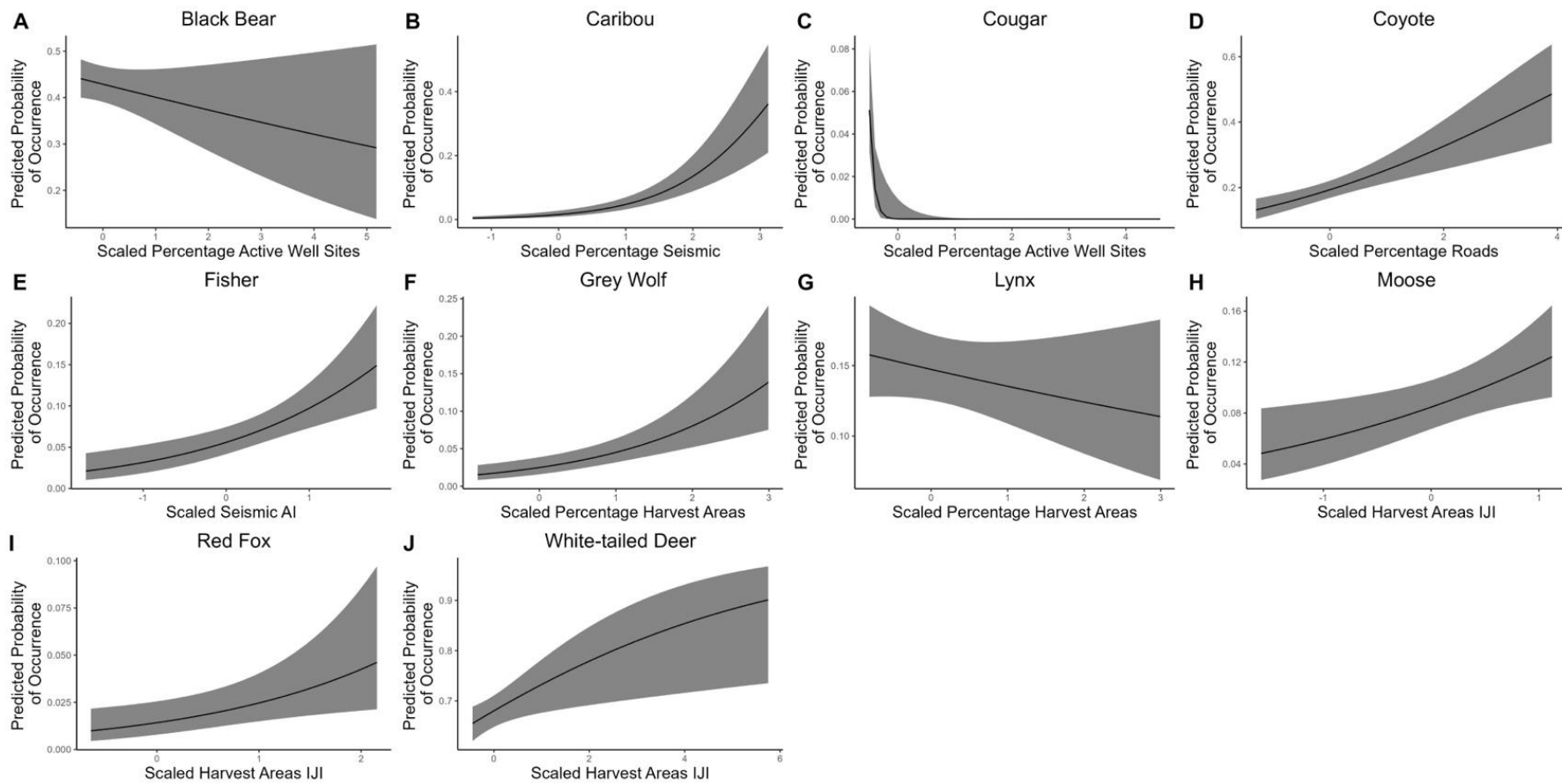


Figure 4. Marginal mean model predictions (and 95% confidence intervals in shaded areas) from the best supported single-variable model for each species. Predicted relationships between predicted probability occurrence of (A) black bear (B) caribou (C) cougar (D) coyote (E) fisher (F) grey wolf (G) lynx (H) moose (I) red fox (J) white-tailed deer and the best supported explanatory variable.

Discussion

We observed mixed responses by species to different OS and non-OS features, manifesting at various scales. This analysis highlights which single features best explain mammal relative abundance in these LUs, but the mixed responses and low explanatory power of many features further emphasizes the need for spatially extensive monitoring across the OSM capturing a range of anthropogenic disturbance, and emphasizes the need for whole community-level analysis (See Section 4).

Black bear distribution was not best explained by any single feature. However, the sum of AIC weight for the OS feature models is 0.76, which is analogous to concluding that 76% of the weight of evidence shows that cumulatively OS features explain black bear distribution, and this outweighs the effects of roads and forest-harvested areas.

Caribou were best explained by an OS feature: seismic lines. While this relationship is predicted to be positive (Figure 4), we caution this result as caribou were only observed in the array which had much more seismic line development. In this sense one should interpret this relationship as “seismic lines are pervasive where caribou occur”, rather than a selection for those lines.

Cougars were observed at 30% of sites in LU2, which was unexpected as this area lays outside their recent range and suggests a northeast expansion. Cougar abundance was best explained OS features – active well sites, abandoned well sites, and industrial sites, together comprising 85% of the weight of evidence. These relationships are negative, reflective of that fact that cougars were detected in the less disturbed landscape, not the more-disturbed landscape. Anecdotally, we observed a large family group on cameras in LU2 (the lower disturbance landscape), which may indicate the presence of breeding individuals in the area, who may prefer lower disturbance areas for raising kittens.

Coyotes were best explained by roads, reflecting results previously observed in the Christina Lake landscape to the north of these LUs^{6,15}.

Fishers were best explained by seismic line aggregation index, and increased with increasing aggregation index. This means that the more aggregated seismic lines were, the probability of fisher occurrence increased. This finding conflicts with past studies showing a

negative response to development¹⁵ and illustrates how context-dependent each species' responses can be.

Wolves were best explained by a combination of harvested areas (40% of weight of evidence) as well as abandoned well sites and seismic lines (53% of weight of evidence together). The positive response to forest harvesting mirrors responses to stressors observed for other features in other areas, and illustrates how this predator is cueing into early seral vegetation patches for herbivore prey^{1,6,9,10,15,16}.

Conversely, lynx were best explained by forest-harvested areas, sharply decreasing with increasing timber harvest. This meshes with Indigenous Knowledge from Whitefish Lake First Nation that says lynx follow hares and other small prey into new stands caused by burning (and harvest), though their camera-trap research also found an effect of well sites⁹.

Moose and red fox both increased with forestry interspersion and juxtaposition index (IJI). This metric describes how forestry (measured as harvested cut blocks) are situated on the landscape amid other anthropogenic features (both OS and non-OS) and land cover classes. An increase in the forestry IJI translates to an increase in the landcover and feature types that forestry cut blocks are adjacent to. Harvested areas provide food for moose and for the small mammal prey that red fox rely on⁴⁶. A positive relationship with a higher IJI could be representative of landscape complementation – when resources a species need are distributed among multiple feature and land cover types and as such, having them juxtaposed to each other could be of benefit^{35,36,66}. Notably red fox distribution is also affected by to seismic lines aggregation index and abandoned well sites (40 % of the weight of evidence).

White-tailed deer distribution is best explained by forestry interspersion and juxtaposition index. Extensive past research has shown that invasive white-tailed deer are strongly attracted to anthropogenic features offering early seral forage subsidy^{2-5,9,12,67,68}. That research suggested multiple forms of disturbance contribute to deer expansion; here we expand on those conclusions to suggests the juxtaposition of forestry with other natural and anthropogenic patch types is strongly contributing to this ecological pattern.

It is important to highlight that this was the first instance of exploring and implementing the use of configuration metrics on an oil sands landscape. As such, a deeper understanding and exploration of configuration metrics, and application to oil-extraction dominant landscapes, is

required to improve our understanding of the related species responses and directly link them to hypothesized ecological processes.

We show that OS landscape features, as single stressors, best explain half of the mammal species we examined. However these are poorly fit models with ample residual error; that is, other factors are also explaining mammals' relative abundance / distribution. In previous works we show how cumulative effects^{4,9,15,69} and species interactions^{2,6,8,10} combine to create the declines (or surpluses) in mammal species compared to a reference, no-disturbance condition. Therefore while this current analysis is useful in affirming the role of OS features, a richer, more accurate explanation is found in the many ecological processes occurring in Alberta's boreal forest. Understanding these complexities and nuances is critical to effective management and restoration to reference conditions, and it is these complexities we explore in Section 4.

4. LARGE-SCALE LANDSCAPE TRAITS ENTRAIN DIFFERENT BOREAL MAMMAL RESPONSES TO ANTHROPOGENIC DISTURBANCE ACROSS THE RAPIDLY DEVELOPING NEARCTIC WESTERN BOREAL FOREST.

OSM Summary

The BADR design is adaptive in nature, in that it stratifies the OSR into high *in situ* disturbance, high mine disturbance, future mine disturbance (current medium-low), and low disturbance landscapes. In the future this will provide the “before-after” component of BADR. Currently, this design provides the “DR” component, a gradient of disturbance for stressor-response modelling. Last year, we asked whether we could expect stressor-responses to be consistent among landscapes. Our analysis in the 2021-2022 Mammals Report provided a clear no (see also Aubertin-Young ⁷⁰). We discovered that stressor-response relationships change from landscape to landscape.

The next natural question then becomes, *how and why do stressor-response relationships change across landscapes?* The BADR design, on full implementation, was created to answer that question. However the implementation of BADR field sampling began only last fiscal year so full analysis of those data will be forthcoming. However, camera-trap data exist from multiple landscapes across Alberta, and we can use these begin answering this question. By combining data from multiple camera arrays⁷¹, each considered a coordinated distributed experiment⁷² of sorts, we can compare stressor-response relationship among arrays, to look for consistencies and differences, each an insight into the causes of observed relationships.

We used data from several mountain and boreal plain arrays and asked how landscape-scale traits such as productivity and overall magnitude of disturbance affect a mammal species’ response to disturbance measured around a camera site. We found clear signals that these landscape-scale traits matter: a species’ response to an OS feature changes with both productivity and degree of disturbance. For example: A moose monitored at a camera with 1% of the surrounding area developed into seismic lines, responds *differently* to those lines if there is overall low landscape disturbance vs. high landscape disturbance. This important result justifies the use of the BADR design wherein sites across the OSR are monitored in rotation. It also helps industry and government target mitigation and restoration efforts to those areas and landscapes where the response is the most negative.

How can this knowledge be used for OSM?

We show that landscape disturbance and productivity affect local-scale mammalian responses to OS features, and we recommend that the current BADR design is necessary to understand the effects of OS development on mammals. We show where focus can be directed as resources require it, and emphasizes the importance of the effects of in-situ development on mammals.

Why did we include data from outside the OSR?

The new BADR program was developed only recently and 2021-2022 was the first year of its field implementation, due to COVID restrictions in past years. Late approvals and the need for a full-year sample prevented 2022-2023 monitoring data from being used in this report. Ergo we capitalized upon existing data from multiple landscapes in the boreal plain and Rocky Mountains that all used designs consistent with BADR Landscape Units (in fact, the LU concept was built on the foundations of these studies), and which contained similar anthropogenic features. Analyses such as the one herein will be applied to future data gathered from LUs across the OSR only, as the program unfolds. The analyses presented here make use of a 10+ year dataset, which lays the framework for proposed analyses of long-term monitoring in the OSR. This paper is drafted as a manuscript submission to *Frontiers in Ecology and Environment*, and is currently undergoing final edits and approvals from coauthors.

Title: Large-scale landscape traits entrain different boreal mammal responses to anthropogenic disturbance across the rapidly developing Nearctic western boreal forest.

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Introduction

Anthropogenic disturbance has led to a global decrease in terrestrial biodiversity, and landscape development is a primary driver of this phenomenon ^{73,74}. Mammals are especially at risk ⁷⁵ and anthropogenic stressors have been linked to behavioural changes through altered diel activity ^{76,77}, population and community changes *via* altered predation rates ^{16,78,79}, and ultimately geographic range reduction for many species ⁸⁰. Mitigating future biodiversity loss requires stopping the mechanisms leading to that loss; however, though patterns of biodiversity losses are everywhere observable, the processes effecting those losses are less clear. Understanding mammalian responses to disturbance is challenging, as ecological processes and the patterns arising therefrom notoriously change across spatial and temporal scales, and among different landscape contexts ⁸¹⁻⁸⁴.

Heuristics exist to contextualize scale- and context-dependency, including Wiens ⁸⁵ ‘domains of scale’ and hierarchy theory, an elegant way of conceiving nestedness and complexity in ecological systems ⁸⁶. Hierarchy theory derives from Aristotelian philosophy and holds that within a *holon* – a self-similar collection of parts that form a functioning whole (from which the term “holistic” originates) – ecological processes operate similarly across a constrained range of spatial scales or conditions ^{87,88}. However, a given holon (H^I) is the sum of smaller, nested holons (H^{II}) plus the emergent properties of the interactions among them. Processes occurring at H^I entrain and constrain processes occurring within the nested smaller holons H^{II} , which themselves entrain and are constructed of even smaller holons H^{III} ⁸⁸. Therefore, differences in ecological processes between multiple locations can potentially be explained by their existence within different holons. We contend that using a macroecological ^{89,90} lens, investigation at smaller scale study sites can be considered lower order holons, while landscapes can be considered as higher order holons (Figure 1). For example, the Western Cordillera of the northern Nearctic exerts a profound effect on the edaphic and hydrologic conditions of the Rocky Mountain front ranges, foothills, and boreal plain. Moist air from the Pacific pulled eastward by Coriolis force mixes with cold air from the Jet Stream directed south by the Cordillera. These air masses are alternately adiabatically cooled and warmed over the mountains and adjacent plain, distributing water heterogeneously over a variable edaphic substrate formed from past erosion and other

geologic processes (H^I , Figure 1). Together these processes induce differences in natural disturbances and plant productivity^{91,92}. As anthropogenic disturbance depends on plant productivity (forestry) and geology (petrochemical extraction) these disturbances are likewise variable within the large scale of H^I . Therefore, the nested smaller scale holons H^{II} landscapes within the mountain foothills and the boreal plain – though are both constrained by the same geoclimatic system (Figure 1), experience different ecological processes and so possess different traits.

Within each H^{II} s there are smaller H^{III} , considered here as a *ca.* 1000 m radius around a survey location (e.g., remote trail cameras, red dots, Figure 1). H^{II} is composed of H^{III} s but also constrains processes (productivity, disturbance) that generate those H^{III} s (Figure 1). Within those landscapes, animals' responses to natural variability and anthropogenic disturbance is constrained by the resources (landscape features) available^{93,94}. Within the boreal plain, moose (*Alces alces*) have available bog, upland deciduous forest, or anthropogenic petroleum exploration (seismic) lines; within mountains, moose have available high-elevation meadows, mid-elevation conifer forests, or lower-elevation valley bottoms and riverine systems (Figure 1). Thus, if we quantify the traits of those H^{II} landscapes, they should explain some variability in mammals' response to features across the multiple H^{III} s of which they are composed.

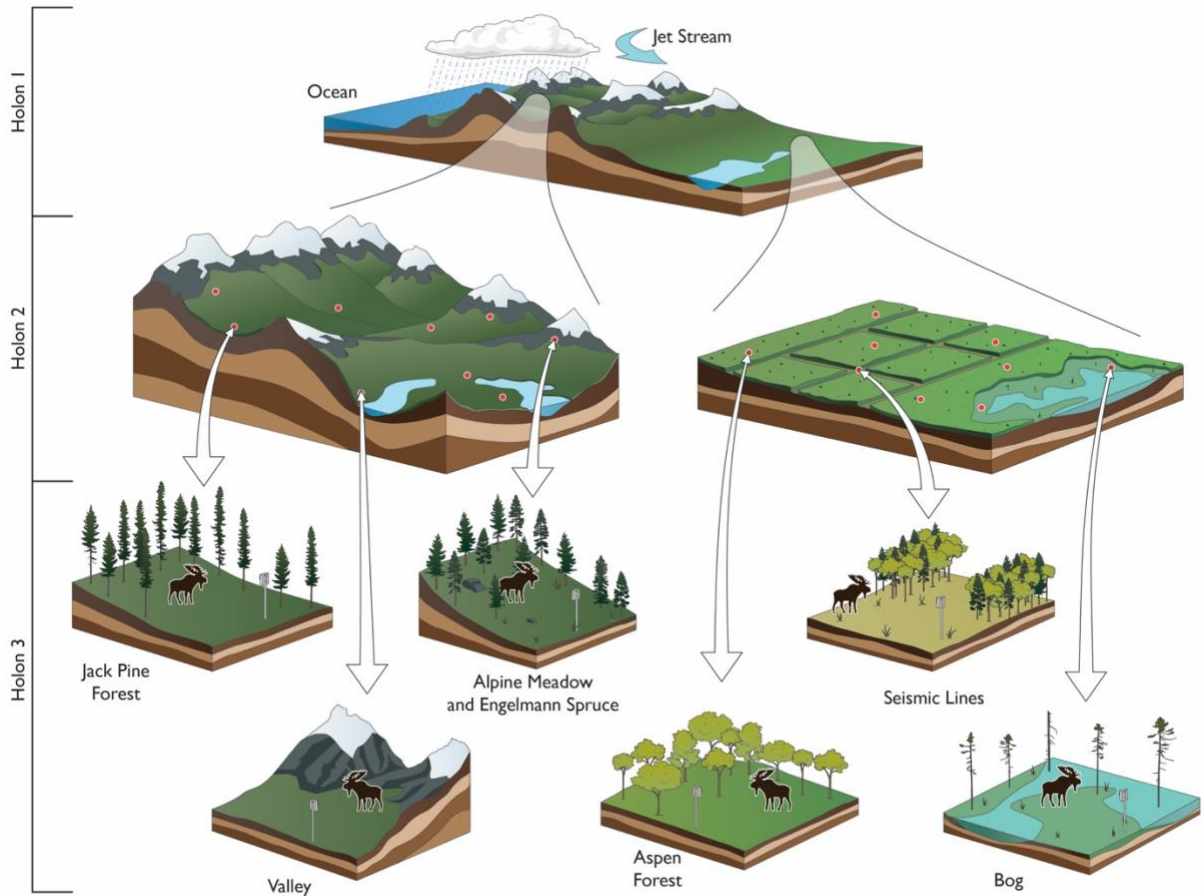


Figure 1. Conceptualizing hierarchy theory as applied to nested landscapes. Holon I is a northern section of the western Cordillera of North America wherein continental-scale hydrologic, meteorologic, and geologic processes shape ecological processes. Holon II are landscapes nested within that region wherein resources are variable, but processes are self-similar within, but different among. Holon III are the areas around camera sites, *e.g.*, a 1000 m² radius, wherein resources are proximal but variable and animals select those resources from choices distributed across the H^{II} landscape. H^I is built from H^{II}s which are built from H^{III}s. In turn H^I processes constrain and entrain H^{II} processes, which do the same for H^{III} processes.

The mediating effect of landscape traits on local species-habitat relationships is conceptually straight-forward but has been historically impossible to quantify for large animals, requiring repeatable data collection over vast distances. However the advent of camera trap technology for wildlife surveys^{95,96} allows investigating multiple research landscapes, scaled-up into a network⁷¹, to sample mammals at point locations (H^{III}) clustered into landscapes (H^{II}), themselves spanning the mountain-boreal complex of western Canada (H^I). This region has seen intense anthropogenic development for forestry, petroleum energy, transportation, and recreation, leading to complex responses across the wildlife community but typically examined only in single landscapes^{9,13,15,97-100}.

Here, we pool weekly presence/absence data for multiple large mammal species data across a span of 13 years and 9 distinct landscapes within the North American western boreal system to test hypotheses about the interaction between holons. Our hypotheses are built around two primary and well-established mammalian responses to disturbance: 1) herbivores exploit the early-succession forage subsidies produced when mature forest is removed for timber or energy^{3,39,40}, and 2) carnivores exploit these aggregations of prey^{16,45}, as well as the movement subsidies offered by cleared linear features such as roads and seismic lines^{37,38}. Given this, we hypothesize herbivores' response to anthropogenic features (the effect size) will be greater in high-productivity landscapes compared to low-productivity landscapes, as vegetation in high-productivity landscapes has the chance to grow more profusely and offer more forage subsidy than lower productivity landscapes. Consequently, carnivores' response to these anthropogenic features will also be greater in high-productivity landscapes. We hypothesize that herbivores' response to local site-level anthropogenic disturbance will be lessened in high-disturbance landscapes. In landscapes saturated by disturbance, the selection for any anthropogenic feature will be weak as there are plenty from which to choose. In contrast, we expect that in low-disturbance landscapes anthropogenic features offer rare resource subsidies that are strongly selected. Likewise, the rarer aggregation of prey at anthropogenic features will produce a stronger carnivore selection for anthropogenic features in low-disturbance landscapes.

Methods

Study Areas

We studied 9 landscapes spanning the western Nearctic boreal in Alberta, Canada: the eastern slopes of the Rocky Mountains (Willmore Wilderness, Yellowhead, Bighorn, and

Kananaskis), central Alberta aspen parkland (Beaverhills Biosphere), and the northern boreal forest (Whitefish Lake, Christina Lake, Richardson Backcountry, and Algar landscape) (Figure S1). Landscapes varied with respect to area, and landcover composition, productivity, and magnitude of anthropogenic disturbances (Table S1, Figure S1).

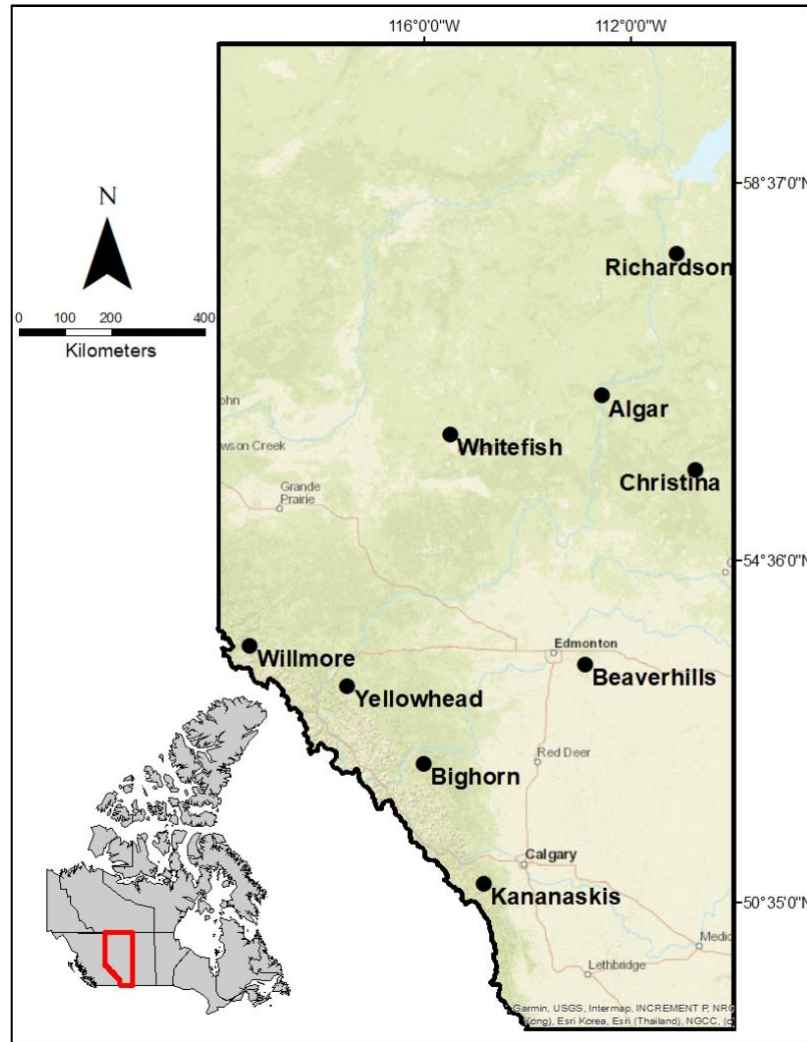


Figure S1. Locations of the nine camera arrays across the boreal and mountain ecoregions of the western Nearctic (within Alberta, Canada).

Cameras were deployed in arrays across each landscape, wherein sampling was originally motivated by unique research goals; although camera setup protocols were similar among landscapes, designs differed (Table S1, references therein). In all cases sampling units were selected using a probabilistic design (systematic or stratified random) spacing cameras apart. Within those units a camera was placed on an active wildlife trail to maximize probability of

species detection given presence. Camera models varied among arrays but were either Reconyx PC900, PC85, PM85, or PM30, Hyperfire I, or Hyperfire II (Reconyx, Holmen, WI, USA) (Table S1). Some arrays used no attractant, others used attractants such as scent lures or bait (Table S1). Cameras were programmed to take a series of photos when movement was detected by the infrared sensor with high sensitivity and fast trigger speed, and operability was determined based off timelapse photos or last photos taken if timelapse was not available (Table S1).

Table S1. Summary and description of camera arrays deployed in Alberta, Canada from 2007-2020.

Landscape	Area (km ²)	Years sampled	N	Total camera trap days	Previously published manuscripts
Algar	570	2015-2019	73	74,218	Beirne et al. ¹⁰¹ : 2015 to 2019 Tattersall et al. ¹² : 2015 to 2019 Tattersall et al. ¹⁰² : 2015 to 2018 Sun, et al. ¹⁰³ : 2016 to 2019
Richardson	604	2017-2019	58	29,526	⁷
Yellowhead	2,388	2012-2014	240	53,434	98,104
Christina	2,494	2011-2014	63	63,475	4,5,8,14,15,100
Bighorn	3,319	2019-2020	83	26,332	¹⁰⁵
Willmore	4,501	2007-2010	118	10,868	61,106
Whitefish	5,101	2018-2020	99	41,151	⁹
Kananaskis	5,362	2011-2014	159	65,508	97,107,108
Beaverhills	1,596	2013-2014 and 2015-16	64	16,123	Stewart, et al. ⁹⁹ : both years of data Stewart, et al. ²⁹ : both years of data Stewart et al. 2018 Ecosphere Burgar et al. 2018 GECCO

Quantifying landscape traits (H^I) and habitat features around cameras (H^{III})

We quantified mean landscape traits, as well as natural and anthropogenic features around camera sites, using a nested approach (Figure S3). We quantified anthropogenic features from the ABMI Human Footprint Inventory ¹⁰⁹⁻¹¹¹, using the temporally closest dataset to camera

sampling for each landscape. Around each camera site we calculated the proportion within a 1-km radius buffer (see Fisher, et al. ⁶¹ for rationale) of active well sites, abandoned well sites, forestry cutblocks, roads, seismic, agricultural, transmission lines, railways, other anthropogenically created linear features, and block (polygonal features). We created a disturbance score for each camera-site (H^{III}) by summing those anthropogenic features (overlapping features create values >1). For each landscape (H^{II}) we then created an overall landscape disturbance score by calculating the mean site disturbance among camera sites.

We quantified landscape H^{II} productivity by classifying individual landscapes into bins of “high” ($> 50\%$ quantile) or “low” ($< 50\%$ quantile) summer plant productivity based on integrated Natural Vegetation Difference Index (NDVI). We quantified natural landscape features around camera sites H^{III} within the 1-km radius buffer around each camera site. We used the Alberta Biodiversity Monitoring Institute (ABMI) Wall-to-Wall Land cover dataset ¹¹² to extract each buffer’s proportion water, shrub, grassland, conifer, broadleaf, and mixed landcover types. To partition variance in mammal occurrence due to non-focal factors, we considered snow cover, seasonality, and topography. We quantified persistent spring snow cover as the mean proportion of years (2000-2020) with spring snow cover (LandSat constant snow cover between April 25 – May 15) within each buffer. Mean elevation and Terrain Ruggedness Index (TRI) were calculated using a digital elevation model. We included season as a categorical variable.

Mammal site-use

Camera images were identified to species using Timelapse 2.0 ³³ or Camelot ¹¹³. We removed sites with < 21 days of camera data to minimize probability of false absences at camera sites. We selected large mammals that were detected in at least 5 of the 9 arrays, and for those that had collectively at least 40 independent detections, to aid model convergence. This filtering process led us to consider 11 species: black bear (*Ursus americanus*), caribou (*Rangifer tarandus*), cougar (*Puma concolor*), coyote (*Canis latrans*), elk (*Cervus canadensis*), grizzly bear (*Ursus arctos*), lynx (*Lynx canadensis*), moose (*Alces alces*), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), and wolf (*Canis lupus*). This species filtering facilitated the cross-landscape comparisons, at the cost of missing array-specific relationships for rarer species. We discretized species detections into weekly presence/absence at each site (Figure S4), which can be interpreted as relative abundance or frequency of site-use (see *Modelling Justification* in SI).

We used package *corrplot*¹¹⁴ to create a correlation matrix and visually examine correlations between continuous variables in our dataset. We detected large Pearson's correlation coefficients (r) between conifer and broadleaf ($r = -0.57$, $p < 0.0001$), snow and elevation ($r = 0.53$, $p < 0.0001$), as well as elevation and TRI ($r = 0.84$, $p < 0.0001$), therefore we removed the variables conifer, and elevation prior to model construction (Figure S5).

We constructed a separate generalized linear mixed model (GLMM) for each species examining weekly presence as a response (Equation 1). The mediating influence of landscape traits on camera-site/mammal relationships was investigated by interacting H^I site disturbance \times H^{II} landscape disturbance, and H^I site disturbance \times H^{II} landscape productivity. We also included variables for each site's proportion of water, shrub, grass, broadleaf, mixed, as well as spring snow and TRI. All continuous variables were scaled to facilitate comparisons between estimated model coefficients and improve computational efficiency. Categorical variables included productivity (where i^{th} level $i = \text{low or high}$), season (where j^{th} level $j = \text{no snow season or snow season}$), baited (where k^{th} level $k = \text{baited camera or not baited camera}$). We included a random effect for Site ID (where l^{th} level $l = \text{individual site}$) and tested for statistically significant improvement of model fit with this random effect structure using likelihood ratio tests¹¹⁵. All models assumed a binomial distribution with a logit link function, and were fit with package *glmmTMB*⁶⁴ using restricted maximum likelihood.

Equation 1:

$$\eta_{ijkl} = \beta_0 + \beta_1 \text{Site Disturbance} \times \text{Landscape Disturbance} \\ + \beta_2 \text{Site Disturbance} \times \text{Landscape Productivity}_i + \beta_3 \text{Site Disturbance} \\ + \beta_4 \text{Landscape Disturbance} + \beta_5 \text{Productivity}_i + \beta_6 \text{Water} + \beta_7 \text{Shrub} \\ + \beta_8 \text{Grass} + \beta_9 \text{Broadleaf} + \beta_{10} \text{Mixed} + \beta_{11} \text{TRI} + \beta_{12} \text{Snow} + \text{Season}_j \\ + \text{Baited}_k + \text{Site ID}_l$$

$$\text{logit}(\pi_{ijkl}) = \eta_{ijkl}$$

$$\text{Weekly Species Presence} \sim \text{Bernoulli}(\pi_{ijkl})$$

$$\text{Site}_i \sim \text{Normal}(0, \sigma_{\text{Site}}^2)$$

We calculated variance inflation factors (VIFs) for each model term using package *performance*¹¹⁶, we removed terms with VIFs > 5 and refit models. For each GLMM, we extracted probability-scale model predictions of weekly species occurrence for the interaction terms of primary interest (site disturbance \times landscape disturbance, and site disturbance \times

landscape productivity) while holding other model terms constant using package *ggeffects*¹¹⁷. We considered estimates of fixed effects to be “significant” when 95% confidence intervals did not overlap zero. All data manipulation and statistical analyses were done using R-Studio v4.2.0⁶².

Results

Across these diverse northern landscapes, we detected 42 mammal species from nine camera arrays from 2007 to 2020. The most frequently detected species were white-tailed deer, black bears, and moose, while the least frequently detected were American badgers (*Taxidea taxus*), bushy-tailed woodrat (*Neotoma cinerea*), and muskrat (*Ondontra zibethicus*) (Table S2). We collected images from 957 sites, representing 380,635 camera trap days.

Seasonal variables and local habitat characteristics variably explain site-scale responses.

The effects of the controlling variables and interaction terms of interest were variable between species (Table S3). Unsurprisingly, season was a statistically significant fixed effect for all species, whereas other fixed effects were only variably important for some species (Table S3). The random effect structure of Site ID significantly improved model fit for all species (Table S4). We removed model terms for local site disturbance and for several species (Table S5), thus omitting those species when making model predictions (see below).

Landscape-level disturbance plays a stronger role than local site disturbance for most species.

Landscape-level disturbance was statistically significant for all species. Higher landscape disturbance led to a statistically significant higher probability of occurrence for all species except black bears ($\beta = -0.3$ [-0.42 – -0.17]) and caribou ($\beta = -1.7$ [-2.2 – -1.21]), although these effect sizes were small across the range of predicted values for some species: < 5% increase for cougars, elk, grizzly bear, moose, and mule deer (Figure S6). Local site disturbance was statistically significant for black bear ($\beta = 0.30$ [0.12 – 0.47]) and white-tailed deer ($\beta = 0.60$ [0.43 – 0.81]); occurrence of both species increased with increasing site disturbance.

The interaction between site and landscape-scale disturbance yielded only four statistically significant trends (two predators and two prey), offering some support for our second hypothesis about feature value increasing with rarity. White-tailed deer were more likely to occur in higher disturbed sites within lower disturbed landscapes ($\beta = -0.30$ [-0.4 – -0.15], Figure 2A),

whereas occurrence was greater in highly disturbed sites within highly disturbed landscapes for moose ($\beta = 0.20$ [0.09 – 0.31], Figure 2B), coyote ($\beta = 0.20$ [0.08 – 0.26], Figure 2C), and lynx ($\beta = 0.20$ [0.07 – 0.26], Figure 2D). For model predictions for all species and accompanying 95% confidence intervals see Figures S7-9).

Landscape productivity mediated mammals' response to local disturbance, variably among predators and prey

We found statistically significant effects of landscape productivity on cougars, coyote, elk, grizzly bears, moose, and mule deer, which all showed a preference for lower productivity landscapes (Table 2). Here again though, effect sizes were small (< 5% for all species, Figure S10). Model predictions for the interaction between site disturbance and landscape productivity showed a much stronger effect for some species (Figure S11). High disturbance sites in high productivity landscapes were preferred by black bears ($\beta = -0.20$ [-0.46 - -0.01], Figure 3A), lynx ($\beta = -0.70$ [-0.97 – -0.34], Figure 3B), and wolves ($\beta = -0.50$ [-0.73 – -0.21], Figure 3C), supporting our hypothesis about carnivores aggregating at disturbed sites in highly productive landscapes. Conversely, this relationship was opposite for mule deer ($\beta = 0.80$ [0.39 – 1.14], Figure 3D), and white-tailed deer ($\beta = 0.20$ [0.01 – 0.47], Figure 3E), who had a higher probability of occurrence in low productivity landscapes with increasing site disturbance.

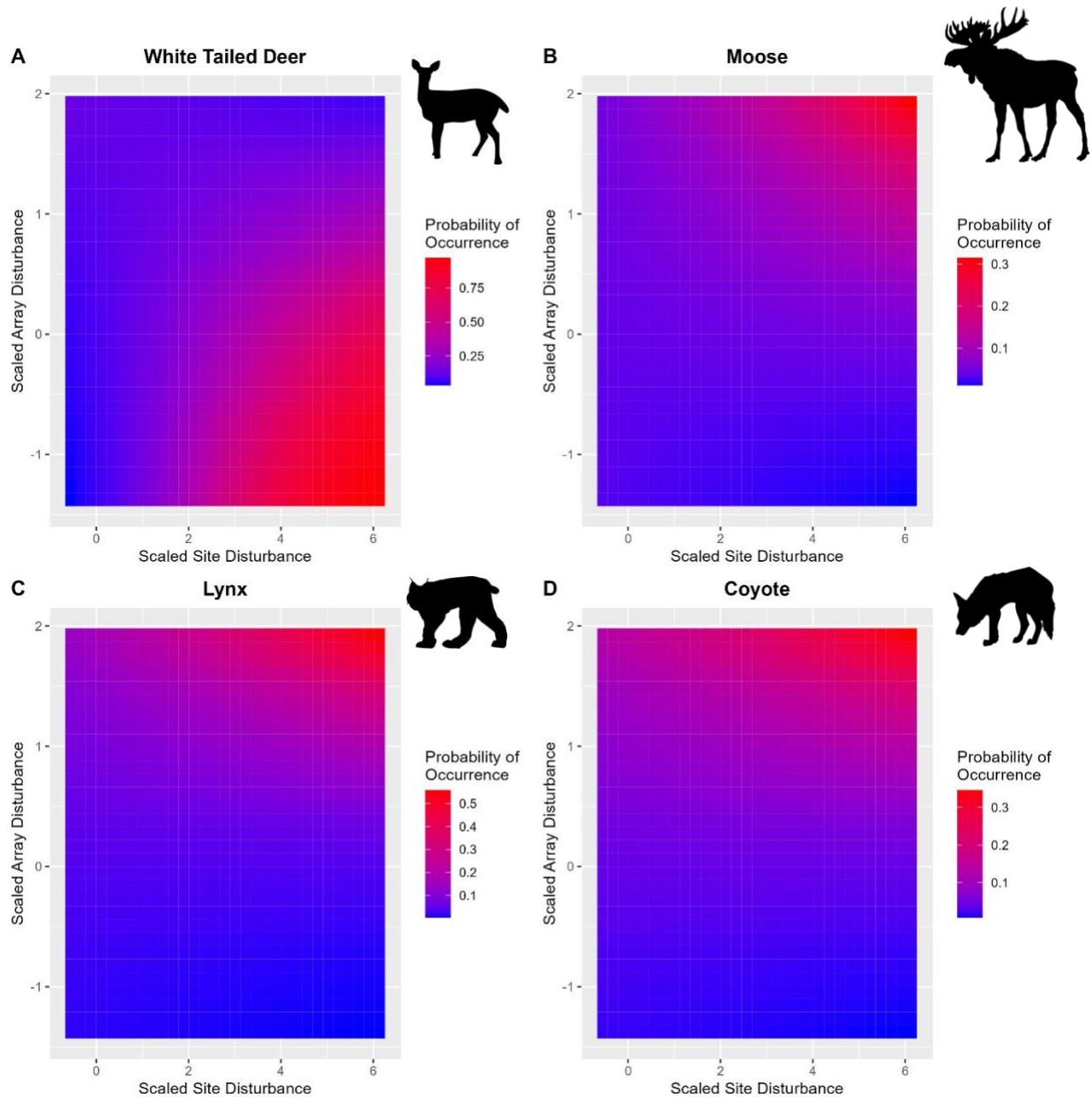


Figure 2. Mean probability scale model predictions for weekly occurrence of A) White Tailed Deer, B) Moose, C) Lynx, and D) Coyote, across the scaled range of array and site disturbance values in our dataset. Note different scales for each species. See Supplemental Materials for upper and lower 95% CI estimates, as well as estimates for complete species set.

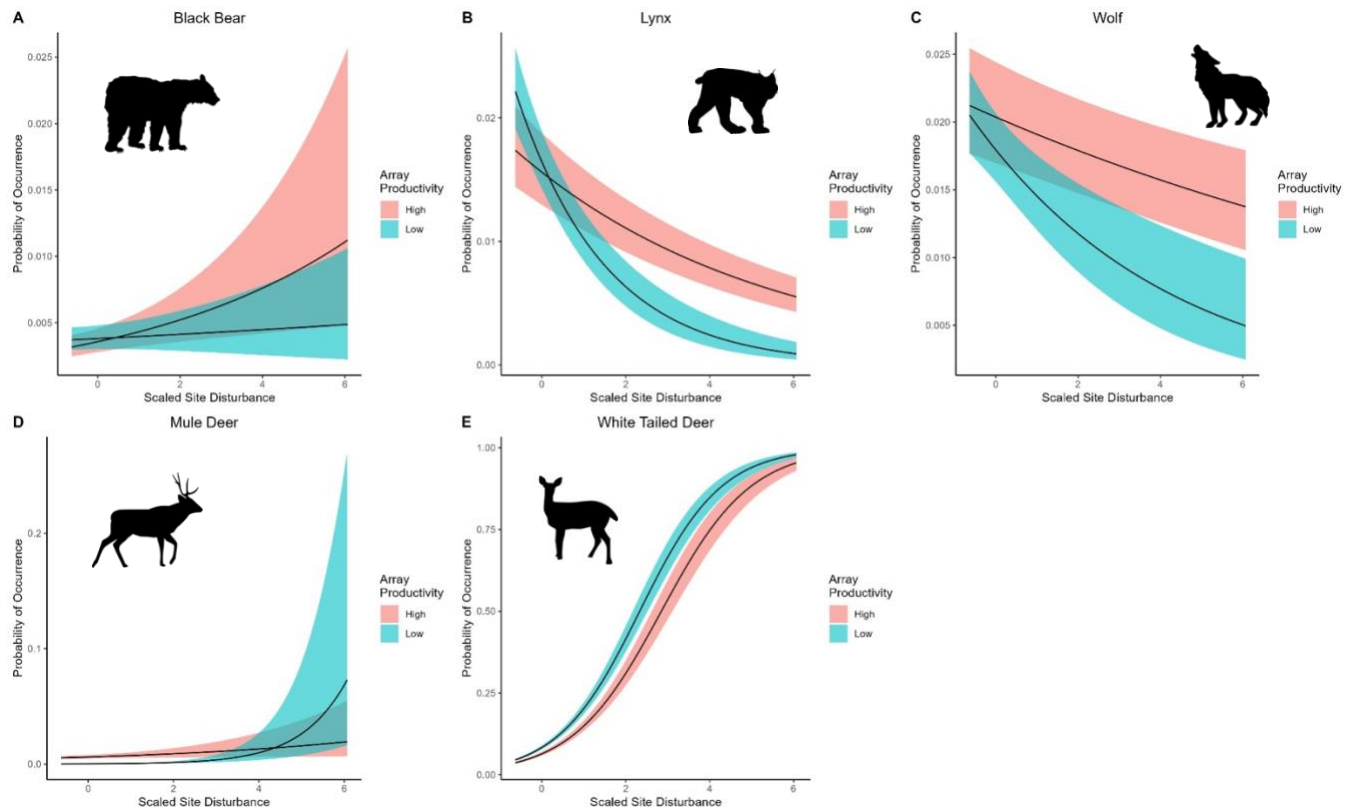


Figure 3. Mean probability scale model predictions (+/- 95% CIs) for weekly occurrence of A) Black bear, B) Lynx, C) Wolf, D) Mule Deer, E) White-Tailed Deer, across the scaled range of site disturbance values and categorical productivity levels. Note different Y-axis scales for each species.

Discussion

Ecological processes occurring at sub-continental scales produce landscapes that vary in productivity and disturbance. In the boreal mountain-plain complex, those landscape traits mediate local-scale responses of mammals to anthropogenic disturbance. By showing differential effects of landscape and site level covariates, we provide evidence in support of hierarchy theory^{86,88} which posits that self-similar, large-scale holons H^I entrain processes occurring at medium-scale nested landscape-scale holons H^{II} , which in turn entrain processes at nested small-scale holons H^{III} (Figure 1). In ecologically meaningful terms, although boreal forest landscapes ca. 3000 km² in size are *de facto* composites of 3000, 1-km² parts, they are more than the sum of those parts. The ecological context created by that aggregate sum (such as high overall landscape disturbance), and by the subcontinental hydrogeological processes in which that landscape is

embedded (such as high landscape productivity), alter mammalian responses to anthropogenic disturbance at local scales. Importantly, these responses also vary by species which has implications for large-scale conservation planning.

Our findings are important for several practical and theoretical reasons. First, understanding species' response to any natural variability is a fundamental goal of ecology, and we anticipate species responses follow some general laws; so far, these are rare ¹¹⁸. Instead we ascribe wide variations in species-habitat relationships (e.g. ³⁶) into the bin of context-dependency and the 'pattern and problem of scale' ⁸¹, with the mechanisms behind this dependency hypothesized ²³ but yet to be discovered. By researching patterns and inferring processes at different spatial scales, we can uncover some of those mechanisms and thereby gain deeper ecological insights.

From a practical perspective, stemming biodiversity loss requires understanding the mechanisms driving that loss. This is especially difficult when disturbance occurs such large scales as the western boreal forest, spanning multiple biomes and ecologies. Conservation actions such as species-at-risk recovery are required but cannot be implemented everywhere due to prohibitive financial and opportunity costs ^{119,120}. As restoration success itself is known to be context-dependent ¹²¹, our hierarchical macroecological approach presents a framework to directs restoration efforts to where they are needed based on generalized findings at scale. For example, based on our findings, targeting restoration to high-disturbance, high-productivity landscapes, would remove the subsidies provided to carnivores that are proximal causes of caribou and other ungulate declines ¹²²⁻¹²⁴, as opposed to spending conservation effort in high-disturbance but low productivity landscapes where predator responses are less strong. Much more work is needed to refine restoration targets and specific conservation actions, and we suggest a hierarchical macroecological approach to understanding species responses to anthropogenic disturbances will substantially aid in targeting restoration efforts ^{125,126}.

Caveats

Our synthetic analysis is derived from camera data acquired from 9 different landscape-scale studies spanning 13 years. The selection of those landscapes was based on project-specific objectives and funding deliverables, and therefore our synthesis does not represent a coordinated design. Undisturbed landscapes are logistically harder to sample and unfortunately underrepresented in our analysis. We advocate again for an international camera-based

biodiversity network ⁷¹ with landscapes allocated to strata “treatments” as coordinated distributed experiments ⁷². We expect that as more arrays are added thereby increasing the data range for disturbance and productivity (and other landscape variables) more and different patterns will emerge. We also note that effect sizes were generally low for landscape-scale variables and the interaction terms we estimated. The 95% confidence intervals often overlapped zero, representing residual error around model estimates. This however is not a problem but an interesting conclusion of its own. Species’ responses to natural features and anthropogenic disturbance are typically examined at landscape scales, and often extrapolated to other portions of a species range. We show that there is very little consistency in species’ responses to those features when modelled across widely divergent landscapes. For example, only black bears and white-tailed deer showed a consistent (positive) response to local-scale disturbance across all the landscapes, despite many studies showing significant within-landscape responses by multiple species (e.g. Fisher, et al. ⁹, Stewart, et al. ⁹⁹, Heim, et al. ⁹⁷, Fisher and Burton ¹⁵). This demonstrates the common “scale problem” of biology ⁸¹: observations made within landscapes do not scale up to produce patterns among multiple landscapes spanning greater ranges of natural and anthropogenic heterogeneity.

Finally, there are multiple technical caveats to this, and any, large analysis. Each project carries its own forms of sampling error, its own subtle differences in designs and deployment and data treatment. The analytical complexities of grouping together disparate datasets are rarely examined in synthetic papers e.g. ^{127,128}, but we expect there are considerable challenges in error propagation throughout these endeavours. We expect that as more camera arrays are *post hoc* ‘networked’ for synthetic analyses these technical issues will become a source of new statistical research and innovations.

Conclusions

The recent call for integrated camera-monitoring networks at broad spatial scales ⁷¹ to ask questions about generalizable macroecological laws ¹¹⁸ has begun to be answered by research examining wildlife responses to anthropogenic stressors across multiple landscapes ¹²⁸⁻¹³³. These collaborative approaches are advantageous as they avoid erroneous extrapolations from findings in single focal populations to adjacent or unrelated systems; if landscapes are treated as fixed effects – with among-landscape variability an “experiment” of its own – mechanisms driving context-dependency and the scale problem can be discovered. While smaller-scale studies using

cameras are inherently valuable and form the basis of many research projects, failing to account for differences in landscape characteristics or other confounding variables when making predictions in other landscapes may lead to spurious conclusions^{132,134}. Indeed, populations of the same species can vary in the magnitude of responses or even show contrasting responses to anthropogenic disturbance¹²⁹. Thus, in the current era of rapid anthropogenic-induced environmental change, making both corroboratory- and anticipatory-predictions of species-specific responses will require careful consideration to better inform conservation efforts.

Acknowledgments

We are extremely appreciative to the personnel responsible for data collection and management for each of the individual camera projects, who are too numerous to name here. Similarly, we are grateful for land access provided by First Nations and private landowners. Funding for this research was provided by the Oil Sands Monitoring Program; this does not represent the views of the program. Individual array project funding was provided by Alberta Environment and Parks, Alberta Biodiversity Monitoring Institute, Alberta Upstream Petroleum Research Fund, Alberta Conservation Association, Algar Caribou Habitat Restoration Program, The Beaver Hills Initiative, Environment and Climate Change Canada, Fur Institute of Canada, InnoTech Alberta, Mitacs, Natural Sciences and Engineering Research Council, Northern Scientific Training Program, Royal Canadian Geographic Society, TD Friends of the Environment Foundation, University of British Columbia, University of Victoria, and Whitefish Lake First Nation #459. Research was legally permitted by Government of Alberta. The creation of the map in Figure S1 was made using the Provinces and Territories of Canada layer and the “Streets” base map using ESRI online (accessed June 28th, 2022). Figure 1 by Jeffdixon.ca under license to JTF. Species silhouettes by G. Chow-Fraser and phylopic.org (accessed June 29th, 2022).

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Supplemental Materials for Large-scale landscape traits entrain different boreal mammal responses to anthropogenic disturbance across the rapidly developing Nearctic western boreal forest.

Table S1. Summary and description of camera arrays deployed in Alberta, Canada from 2007-2020.

Landscape	Area (km²)	Years sampled	N	Total camera trap days	Attractant used?	Timelapse Photos	Site description
Algar	570	2015-2019	73	74,218	No	Yes	Smallest array, low elevation, and relatively flat landscape. Dominant landcover conifer forest. Dominant disturbance is seismic exploration features.
Richardson	604	2017-2019	58	29,526	No	Yes	Northernmost array, low elevation, and relatively flat landscape. Dominant landcover conifer forest. Very little anthropogenic disturbance.
Yellowhead	2,388	2012-2014	240	53,434	No	No	High elevation landscape with rough terrain. Dominant landcover conifer forest, dominant disturbance is forestry cutblocks.
Christina	2,494	2011-2014	63	63,475	No	No	Easternmost array. Mid-elevation array. Dominant landscape conifer and broadleaf forest. Dominant disturbance is well sites and seismic exploration lines.
Bighorn	3,319	2019-2020	83	26,332	No	Yes	High elevation landscape with rough terrain. Dominant landcover conifer forest, dominant disturbance is forestry cutblocks.
Willmore	4,501	2007-2010	118	10,868	Yes	Yes	Westernmost array, high elevation landscape with rough terrain. Dominant landcover is conifer forest. Very little anthropogenic disturbance.
Whitefish	5,101	2018-2020	99	41,151	No	Yes	Mid-elevation array. Dominant landscape conifer and broadleaf forest. Dominant disturbance is well sites and seismic exploration lines.
Kananaskis	5,362	2011-2014	159	65,508	Yes	No	Southernmost and largest array, high elevation landscape with rough terrain. Dominant landcover conifer forest, dominant disturbance is forestry cutblocks.

Landscape	Area (km²)	Years sampled	N	Total camera trap days	Attractant used?	Timelapse Photos	Site description
Beaverhills	1,596	2013-2014 and 2015-16	64	16,123	Yes	No	Dominant landcover boreal and broadleaf aspen parkland. Array was baited with 5kg chunks of beaver carcasses and scent lure, with genetic hair snags also included at sites sensu the Kananaskis and Wilmore arrays

Table S2 Summary of species detections from nine monitoring arrays in Alberta, Canada from 2007 to 2020. Total detections are the number of images captured with species in frame, whereas independent detections are detections separates by ≥ 30 minutes.

SPECIES	TOTAL DETECTIONS	TOTAL INDEPENDENT DETECTIONS
WHITE-TAILED DEER	159040	22011
HUMAN	28967	16165
BLACK BEAR	21966	4390
MOOSE	19281	2405
COYOTE	10375	3800
SNOWSHOE HARE	9660	5601
CARIBOU	6737	845
MULE DEER	6666	2032
GRIZZLY BEAR	4380	1416
WOLF	4250	2085
ELK	3107	1405
LYNX	3059	2014
RED SQUIRREL	2338	1628
RED FOX	1662	1046
FISHER	803	103
BIGHORN SHEEP	557	111
MARTEN	537	385
COUGAR	409	314
MARMOT	381	144
WOLVERINE	208	46
GOLDEN-MANTLED GROUND SQUIRREL	157	63
FLYING SQUIRREL	148	63
BOBCAT	120	107
STRIPED SKUNK	43	35
PORCUPINE	41	21
COLUMBIAN GROUND SQUIRREL	36	7
MOUNTAIN GOAT	26	7
RABBIT	26	5
RIVER OTTER	17	12
BEAVER	11	4
BISON	10	1
CHIPMUNK	7	7
RICHARDSON'S GROUND SQUIRREL	7	5
WEASEL	7	2
RACCOON	5	5
SHORT-TAILED WEASEL	5	2
MINK	4	2

GROUNDHOG	2	1
PIKA	2	2
BADGER	1	1
BUSHY-TAILED WOODRAT	1	1
MUSKRAT	1	1

Modelling Justification

We used generalized linear models with serial detection data (e.g., 1010110) as the response metric. We elected not to use occupancy models²⁶ as some authors recommend. We have used these in the past^{106,135-138} and indeed our work is highlighted in the Second Edition of the textbook. However, these models assume that in a mixed detection history of 1s and 0s those 0s are error. Instead, we consider 0s within a week-long period as evidence of temporary emigration, rather than missed detection. Missing an animal (if present) repeatedly within a week-long period is highly unlikely given the deployment of attractants, the mobility of all species we studied, and reliability of the cameras used which we evaluated using camera operability matrices). Temporary emigration is a part of the site-use process we wish to model, function of species' movement rates and local density¹³⁹⁻¹⁴¹, and so we treated 0s as true zeros in GLMs and not error, as occupancy models treat 0s.

Further, we considered serial detection histories from within a camera site as being more similar than detection histories among camera sites (Tobler's First Law), and hence we used a random effect to account for any such similarity not due to fixed effects^{142,143}. The random effect (unlike fixed effects) is considered to be drawn from a larger population of which the random variable is a subsample^{144,145}; here our study sites are small samples drawn from the much larger northwestern Nearctic.

Table S3 Parameter estimates from generalized linear mixed models for each species. Estimates provided with lower and upper 95% CI; random effect estimates presented as standard deviation. Bold values for fixed effects represent estimates in which 95% CI do not overlap zero. NA values represent model terms which were removed due to variance inflation factors > 5, see Table S5.

Parameter	Black Bear	Caribou	Cougar	Coyote	Elk	Grizzly Bear	Lynx	Moose	Mule Deer
Intercept	-6.2 [-6.46– -5.91]	-8.3 [-8.96– -7.65]	-5.3 [-5.68– -4.97]	-3.6 [-3.91– -3.39]	-5.8 [-6.24– -5.31]	-6.3 [-6.68– -5.96]	-4.5 [-4.79– -4.19]	-3.6 [-3.82– -3.42]	-5.2 [-5.47– -4.84]
Site Disturbance	0.3 [0.12– 0.47]	NA	NA	NA	0.2 [-0.19– 0.54]	0.1 [-0.08– 0.31]	NA	-0.1 [-0.22– 0.12]	0.1 [-0.15– 0.3]
Array Disturbance	-0.3 [-0.42– -0.17]	-1.7 [-2.2– -1.21]	0.5 [0.31– 0.66]	1 [0.81– 1.1]	0.7 [0.4– 0.91]	0.5 [0.33– 0.61]	0.8 [0.68– 0.99]	0.3 [0.2– 0.43]	0.6 [0.48– 0.8]
Productivity*	0.1 [-0.24– 0.37]	NA	-3.3 [-4.15– -2.44]	-1.1 [-1.51– -0.64]	-4 [-5.21– -2.85]	-4.3 [-5.45– -3.14]	0 [-0.5– 0.44]	-0.6 [-0.97– -0.33]	-3.3 [-4.09– -2.57]
Site x Array Disturbance	0 [-0.15– 0.08]	0.1 [-0.44– 0.57]	0 [-0.11– 0.09]	0.2 [0.08– 0.26]	-0.2 [-0.49– 0.03]	0 [-0.19– 0.09]	0.2 [0.07– 0.26]	0.2 [0.09– 0.31]	0 [-0.19– 0.12]
Site Disturbance x Productivity	-0.2 [-0.46– -0.01]	NA	0.4 [-0.13– 0.99]	0.2 [-0.06– 0.44]	0.3 [-0.46– 0.98]	0.4 [-0.51– 1.24]	-0.7 [-0.97– -0.34]	-0.1 [-0.26– 0.13]	0.8 [0.39– 1.14]
Water	0.2 [0.09– 0.28]	-0.7 [-1.32– -0.07]	0.2 [0.03– 0.35]	0.2 [0.1– 0.33]	0.3 [0.12– 0.54]	0.1 [-0.03– 0.23]	-0.3 [-0.43– -0.09]	0 [-0.09– 0.1]	0.3 [0.12– 0.4]
Shrub	0.1 [-0.06– 0.17]	0 [-0.26– 0.27]	-0.2 [-0.47– -0.03]	-0.3 [-0.51– -0.17]	0 [-0.28– 0.31]	-0.1 [-0.22– 0.09]	-0.1 [-0.23– 0.11]	-0.1 [-0.25– -0.02]	-0.1 [-0.3– 0.05]
Grass	0 [-0.14– 0.08]	0.3 [0– 0.52]	0.3 [0.1– 0.43]	0.3 [0.15– 0.43]	0.4 [0.13– 0.59]	0.1 [-0.06– 0.2]	0 [-0.14– 0.19]	0 [-0.09– 0.12]	0 [-0.17– 0.16]
Broadleaf	0.1 [0.01– 0.26]	-0.6 [-1.2– 0.08]	0.1 [-0.18– 0.47]	0.1 [-0.09– 0.23]	0.8 [0.49– 1.2]	-0.1 [-0.47– 0.24]	-0.8 [-1.02– -0.57]	0.3 [0.15– 0.38]	0.3 [0.09– 0.6]
Mixed	0.1	-0.8	0.1	0.4	0	0.1	0	0	-0.1

Parameter	Black Bear	Caribou	Cougar	Coyote	Elk	Grizzly Bear	Lynx	Moose	Mule Deer
	[-0.04–0.19]	[-1.2–-0.38]	[-0.09–0.33]	[0.2–0.51]	[-0.32–0.34]	[-0.13–0.25]	[-0.14–0.22]	[-0.1–0.14]	[-0.3–0.12]
TRI	0.1	-1.5	0.4	0	0.3	0.4	-0.3	-0.2	0.6
	[-0.03–0.29]	[-2.1–-0.89]	[0.21–0.6]	[-0.24–0.18]	[0.01–0.65]	[0.27–0.59]	[-0.49–-0.01]	[-0.39–-0.07]	[0.42–0.81]
Snow	-0.4	NA	-0.5	-0.2	-0.2	0.1	-0.1	0.1	-0.3
	[-0.58–-0.29]		[-0.76–-0.3]	[-0.35–-0.02]	[-0.39–0.07]	[0.02–0.22]	[-0.35–0.06]	[-0.05–0.18]	[-0.42–-0.13]
Season	3.5	1.2	0.5	0.5	1.5	2.7	0.3	0.7	1.7
¥	[3.29–3.71]	[1.04–1.38]	[0.29–0.8]	[0.4–0.58]	[1.26–1.79]	[2.38–2.93]	[0.2–0.41]	[0.65–0.84]	[1.48–1.88]
Bait	-0.2	0.6	0.4	0.1	0	0.3	0.1	-0.1	-0.8
€	[-0.47–0.01]	[-0.84–2]	[0.07–0.73]	[-0.03–0.28]	[-0.35–0.26]	[0.11–0.54]	[-0.29–0.44]	[-0.26–0.1]	[-1.07–-0.5]
Site ID	1.1	2.1	1.1	1.6	2.1	1	1.7	1.2	1.4
	[1.02–1.21]	[1.74–2.51]	[0.89–1.28]	[1.48–1.75]	[1.86–2.39]	[0.91–1.16]	[1.53–1.83]	[1.11–1.31]	[1.26–1.55]

*Reference category is “low” productivity

¥ Reference category is “snow” season.

€ Reference category is “not baited” camera stations.

Table S4 Likelihood Ratio Test parameters for each species' GLMM.

SPECIES	DF	X2	P
BLACK BEAR	1	1303.948	< 0. 0001
CARIBOU	1	634.7474	< 0. 0001
COUGAR	1	82.30749	< 0. 0001
COYOTE	1	2816.238	< 0. 0001
ELK	1	1122.871	< 0. 0001
GRIZZLY BEAR	1	531.4664	< 0. 0001
LYNX	1	1740.18	< 0. 0001
MOOSE	1	1545.294	< 0. 0001
MULE DEER	1	1145.065	< 0. 0001
WHITE TAILED DEER	1	7919.699	< 0. 0001
WOLF	1	1286.675	< 0. 0001

Table S5 Variance Inflation Factors (VIFs) for model terms in GLMMs constructed for each species. Bolded values represent terms with VIFs > 5 which were removed from subsequent models.

MODEL TERM	BLACK BEAR	CARIBOU	COUGAR	COYOTE	ELK	GRIZZLY BEAR	LYNX	MOOSE	M	DI
SITE DISTURBANCE	4.6	1742.8	5.04	5.01	4.4	4.5	5.6	4.7		
ARRAY DISTURBANCE	1.7	3.3	1.2	1.5	1.3	1.4	1.6	1.8		
PRODUCTIVITY	2.3	908	2	2.8	3.2	1.3	2.5	2.5		
WATER	1.1	1	1.1	1.1	1.2	1.1	1.1	1.1		
SHRUB	1.4	1.6	1.2	1.2	1.3	1.3	1.3	1.3		
GRASS	1.2	1.4	1.3	1.2	1.2	1.3	1.3	1.2		
BROADLEAF	1.5	1.2	1.7	1.8	2.7	1.3	1.6	1.8		
MIXED	1.2	1.1	1.2	1.2	1.1	1.2	1.2	1.2		
TRI	2.5	4	1.7	2.6	2	1.7	2.6	2.7		
SNOW	1.4	5.3	1.3	1.5	1.5	1.8	1.5	1.6		
SEASON	1	1	1.2	1.1	1.1	1.1	1	1.1		
BAIT	1.1	2.7	1.2	1.1	1.1	1.2	1.2	1.2		
SITE_DISTURBANCE X ARRAY_DISTURBANCE	3.6	2.4	4.7	4.2	4.3	4.5	4.6	3.8		4
SITE_DISTURBANCE X PRODUCTIVITY	1.5	1662	1.4	1.5	1.2	1.2	1.5	1.5		

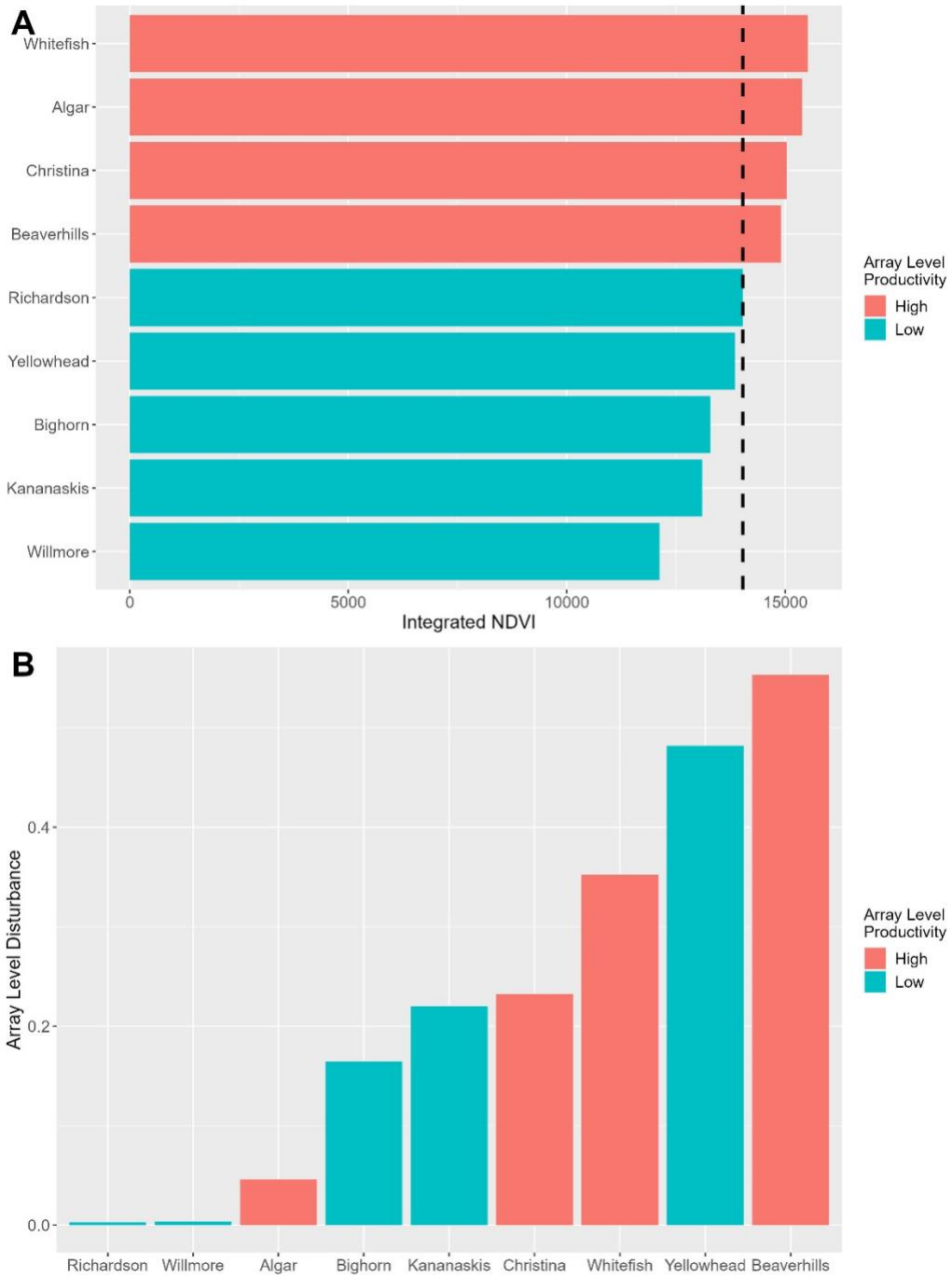


Figure S2 Summaries of A) array level productivity compared to integrated NDVI values. Black-dashed line represents 50% quantile of data. B) array level productivity compared to array level disturbance.

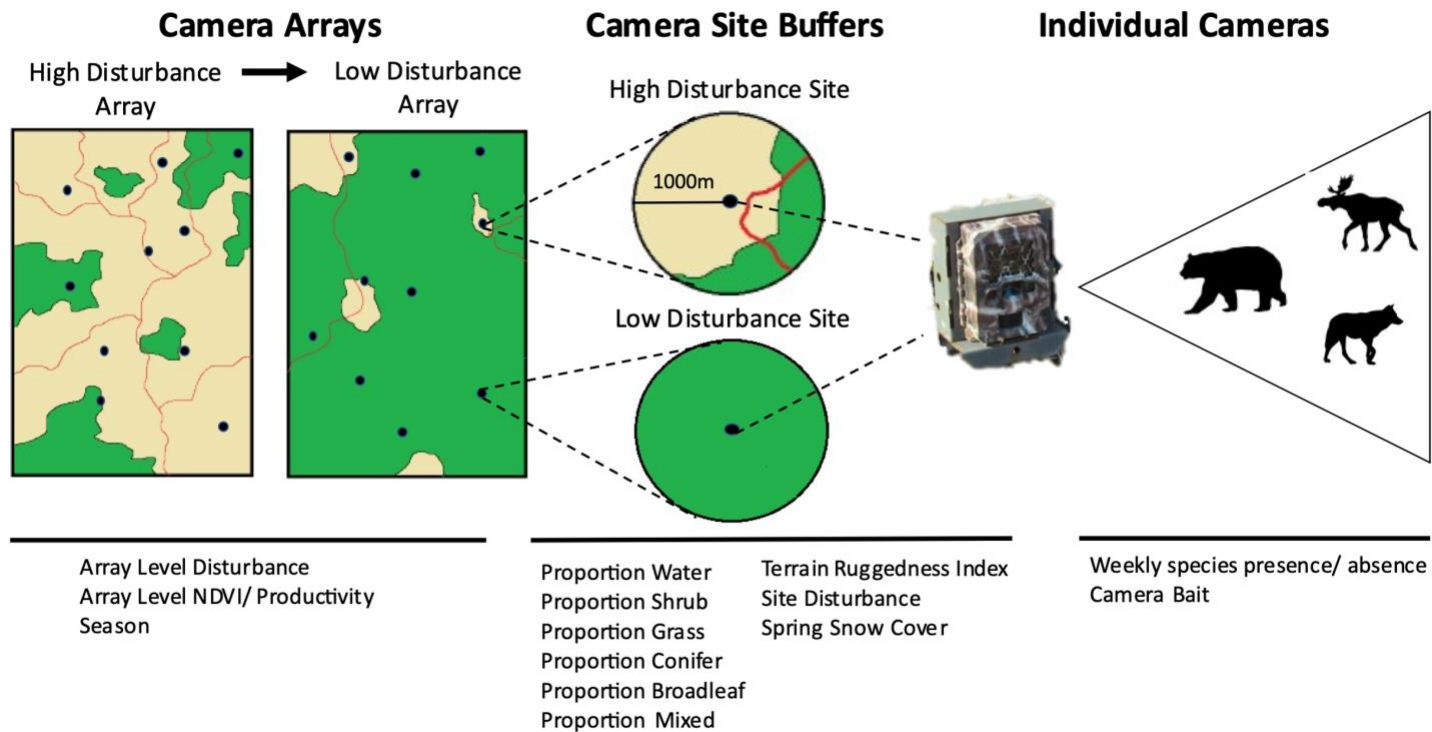


Figure S3. Heuristic of the nested sampling structure: camera array (landscape H^{II}) for which we calculated landscape traits; camera site buffered area (H^{III}) within which landscape features were quantified; and individual cameras that detected weekly presence/absence for multiple mammal species. Green and tan colors in arrays and camera site buffers represent disturbed and undisturbed habitat respectively, while red lines represent example linear disturbance features (e.g., seismic lines or roads).

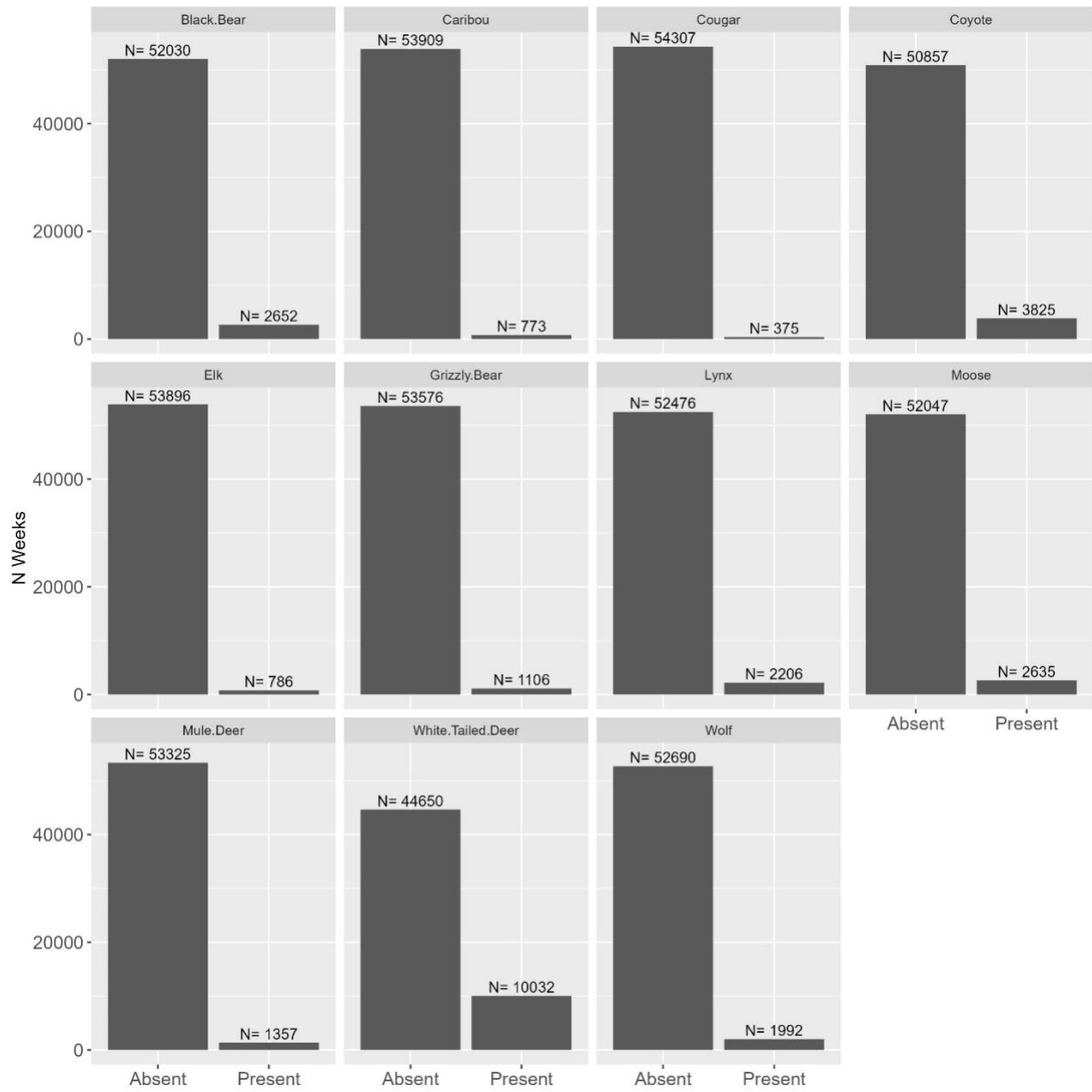


Figure S4 Number of weeks of absence or presence for modelled species

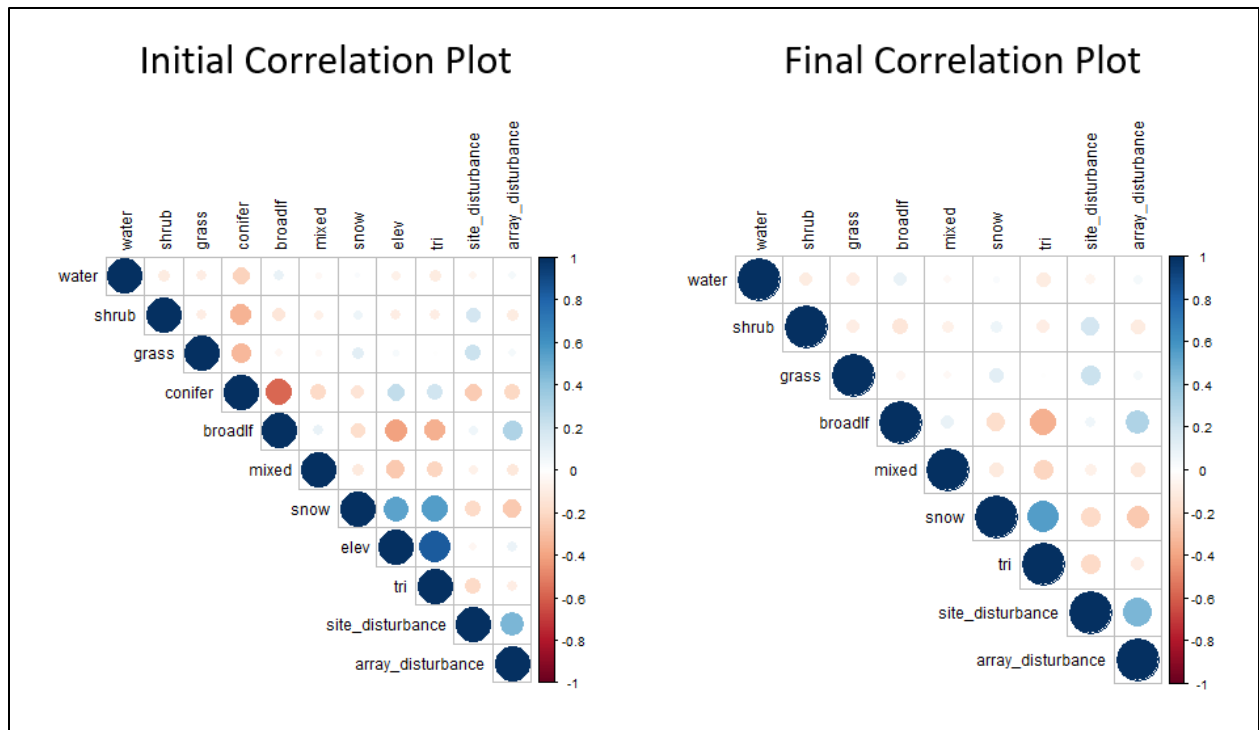


Figure S5 Initial and final correlation plots for site and array habitat characteristics. Final correlation plot indicates variables retained after removing conifer, and elevation from the dataset.

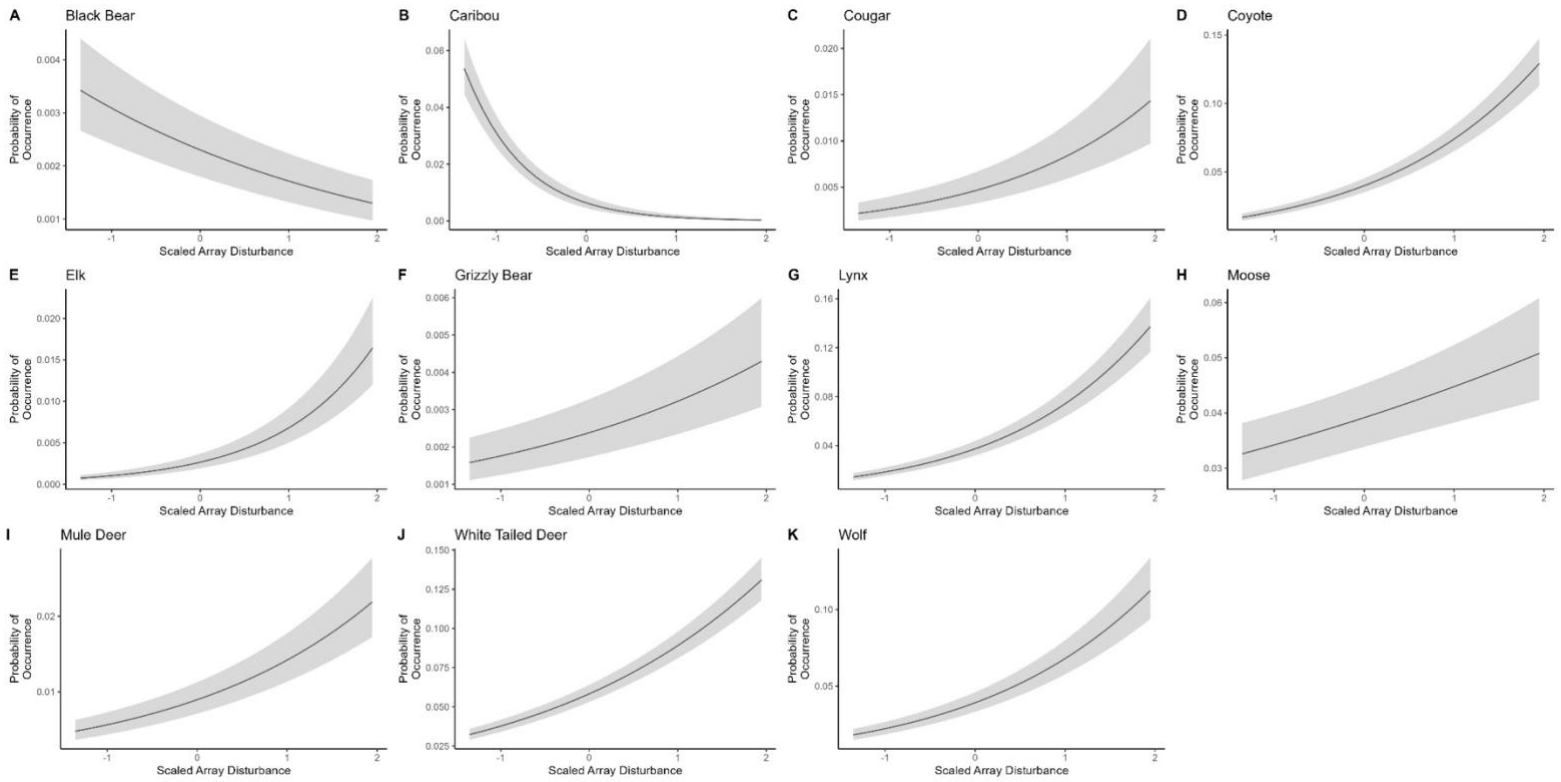


Figure S6 Mean probability scale model predictions for weekly occurrence of A) Black bear, B) Caribou, C) Cougar, D) Coyote, E) Elk, F) Grizzly Bear, G) Lynx, H) Moose, I) Mule Deer, J) White-Tailed Deer, K) Wolf, across the scaled range of array disturbance values in our dataset. Note different scales for each species.

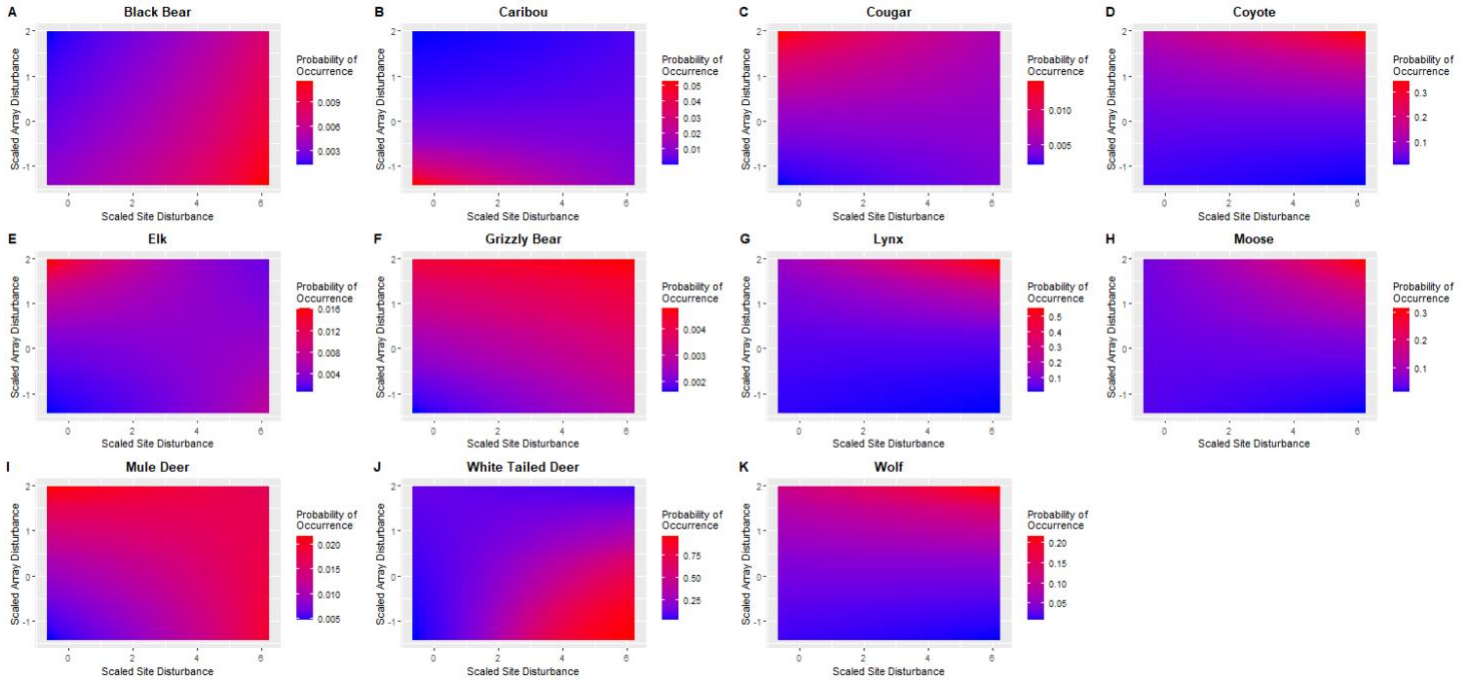


Figure S7 Mean probability scale model predictions for weekly occurrence of A) Black bear, B) Caribou, C) Cougar, D) Coyote, E) Elk, F) Grizzly Bear, G) Lynx, H) Moose, I) Mule Deer, J) White-Tailed Deer, K) Wolf, across the scaled range of array and site disturbance values in our dataset. Note different scales for each species. See Figures S8 and S9 for upper and lower 95% CI estimates.

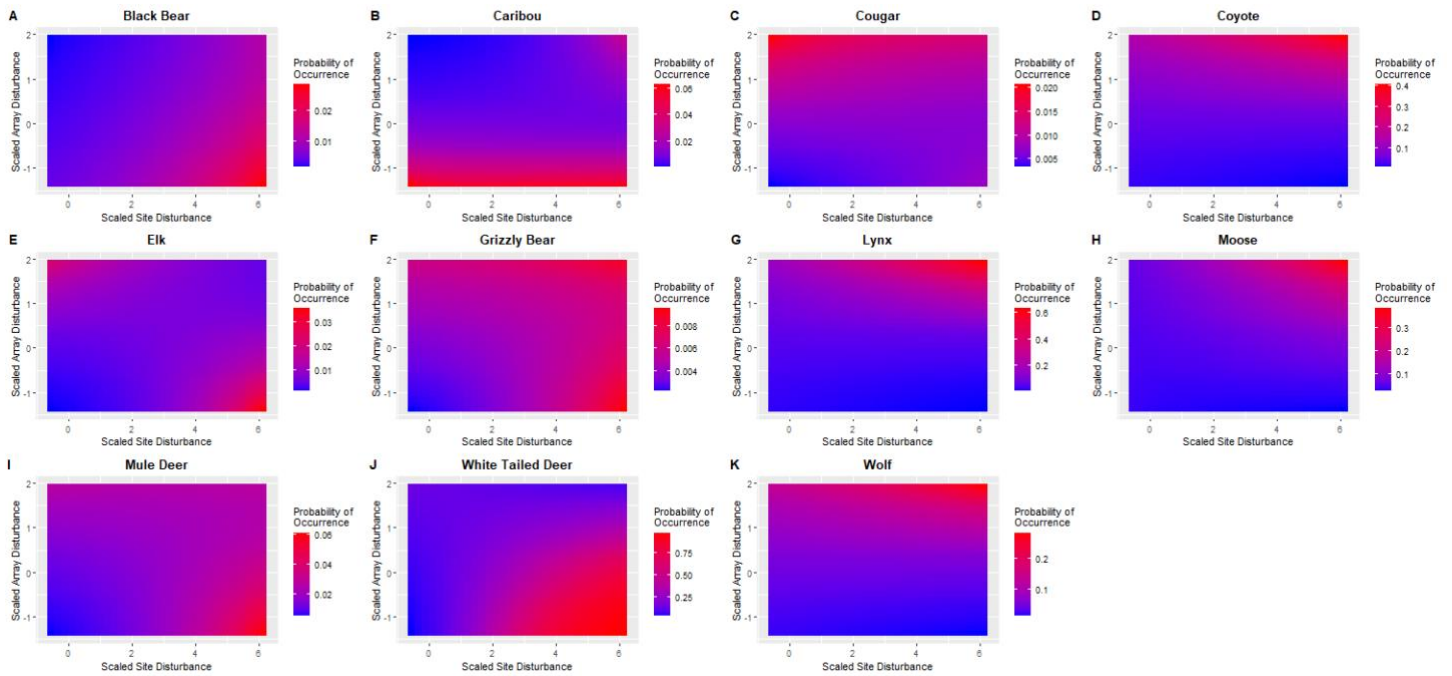


Figure S8 Upper 95% confidence interval probability scale model predictions for weekly occurrence of A) Black bear, B) Caribou, C) Cougar, D) Coyote, E) Elk, F) Grizzly Bear, G) Lynx, H) Moose, I) Mule Deer, J) White-Tailed Deer, K) Wolf, across the scaled range of array and site disturbance values in our dataset. Note different scales for each species. See supplemental materials for upper and lower 95% CI estimates.

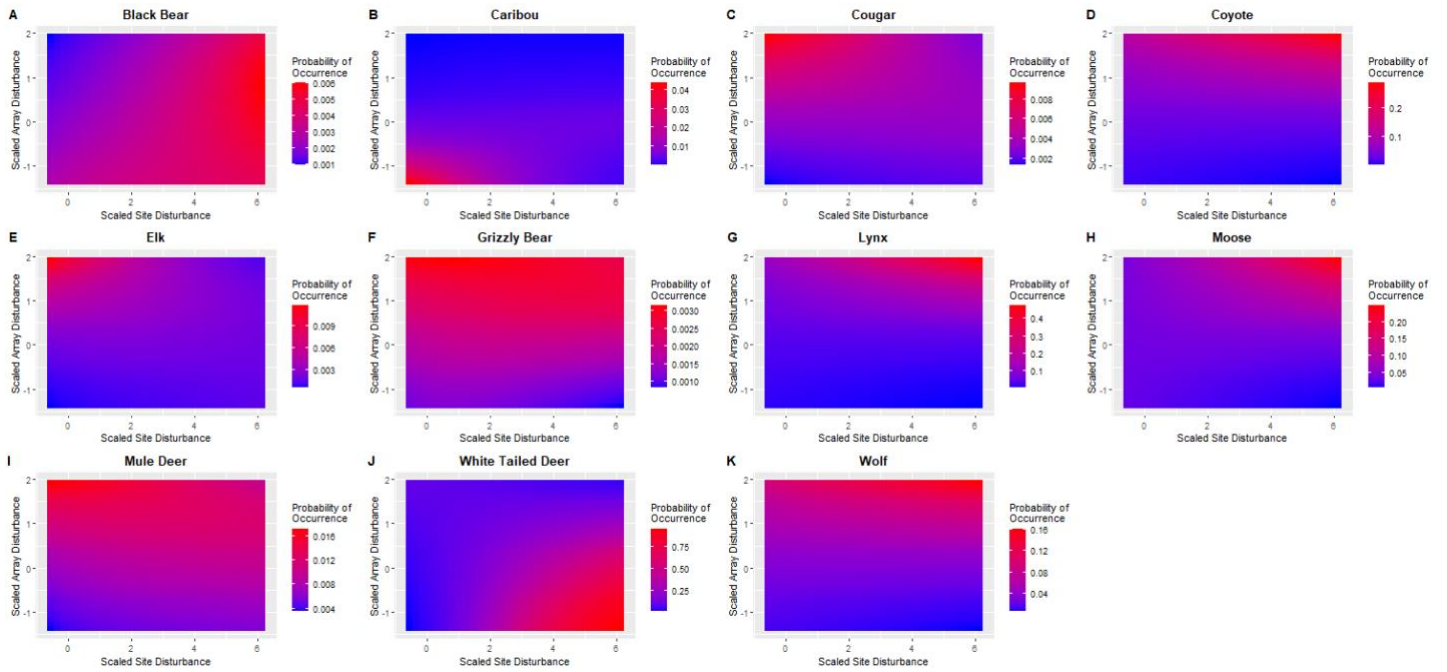


Figure S9 Lower 95% confidence interval probability scale model predictions for weekly occurrence of A) Black bear, B) Caribou, C) Cougar, D) Coyote, E) Elk, F) Grizzly Bear, G) Lynx, H) Moose, I) Mule Deer, J) White-Tailed Deer, K) Wolf, across the scaled range of array and site disturbance values in our dataset. Note different scales for each species. See supplemental materials for upper and lower 95% CI estimates.

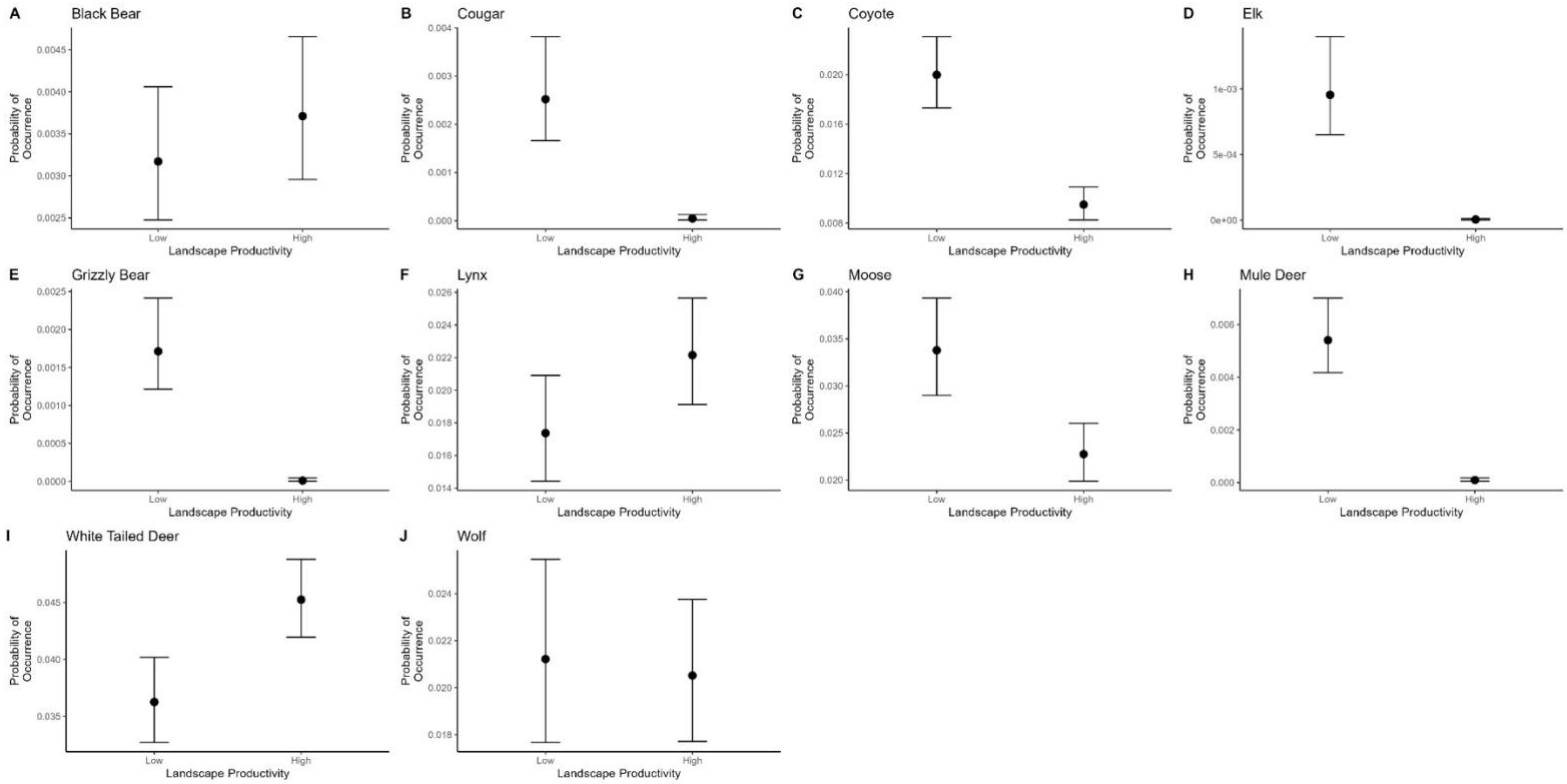


Figure S10 Mean probability scale model predictions for weekly occurrence of A) Black bear, B) Cougar, C) Coyote, D) Elk, E) Grizzly Bear, F) Lynx, G) Moose, H) Mule Deer, I) White-Tailed Deer, J) Wolf, in low and high productivity landscapes. Note different scales for each species.

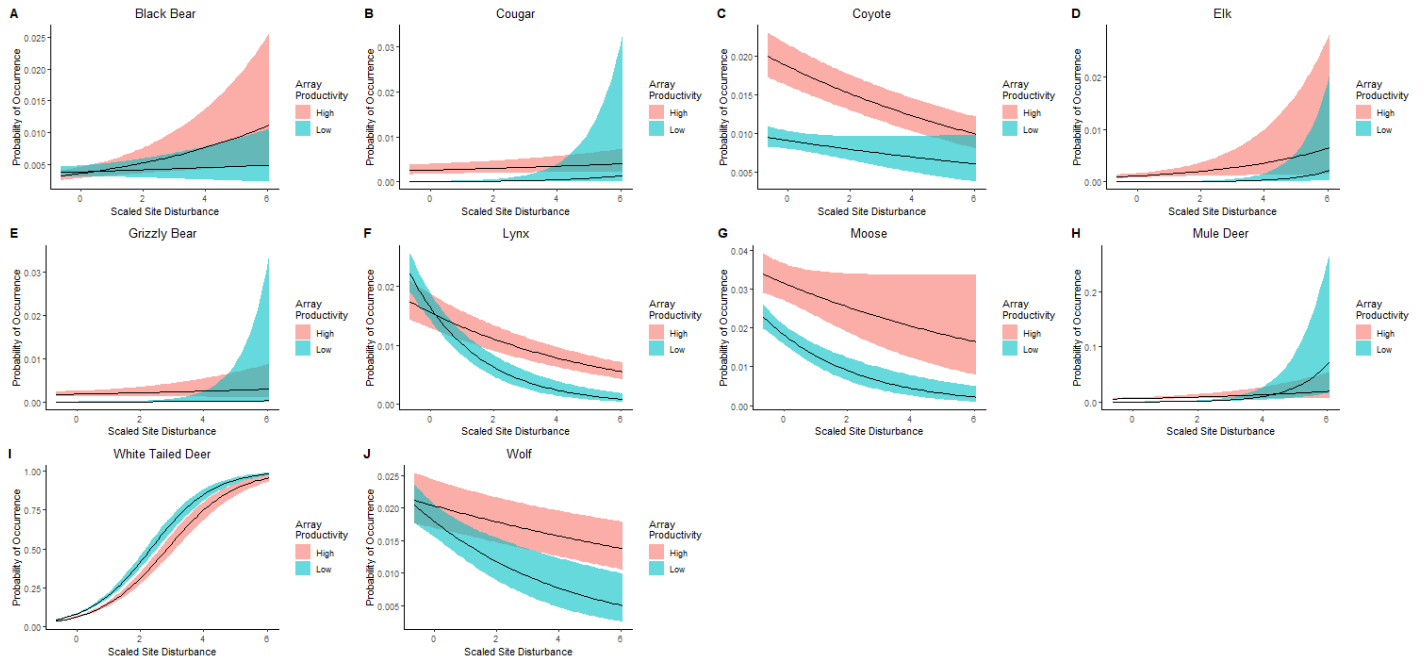


Figure S11 Mean probability scale model predictions for weekly occurrence of A) Black bear, B) Cougar, C) Coyote, D) Elk, E) Grizzly Bear, F) Lynx, G) Moose, H) Mule Deer, I) White-Tailed Deer, J) Wolf, across scaled site disturbance in low and high productivity landscapes. Note different scales for each species.

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