



# OIL SANDS MONITORING: MAMMALS 2021-2022 TECHNICAL REPORT

DR. JASON T FISHER  
TERRESTRIAL BIOLOGICAL MONITORING TEAM

DR. ANDREW BARNAS  
DR. ANDREW LADLE  
MACGREGOR AUBERTIN-YOUNG  
KATHERINE BAILLIE-DAVID  
SEAN MURRAY  
REBECCA SMITH  
SANDRA FREY  
H. WILEMAN FULLER

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## MAIN MESSAGES FOR OIL SANDS MONITORING

The ACME Lab's OSM Mammal Monitoring program was funded at 66% of requested budget in 2021-2022. Within this budget we delivered on field monitoring for two of the four proposed Landscape Units under the BADR design, and we provided proactive advice tailored to ongoing discussions within the TBM TAC. Here we report the summary statistics from that program. Further data analyses are proposed for 2022-2023. In the interim we used existing data from ongoing research programs in the OSR and beyond to answer questions that have been posed last year in discussions among the TBM team and the TAC.

The first obvious question is: what is gained by monitoring multiple landscapes under the BADR design? Can we be more efficient monitoring a few representative landscapes? Our analysis suggests no, we cannot expect a few landscapes to represent the entire OSM. Stressor-response relationships – which sit at the core of the TBM conceptual model – change among landscapes, with different contexts. This conclusion emphasizes the importance of the multiple landscape units identified under the BADR design, implemented across the OSR.

The second question is: how much of an impact are OS features having on mammal diversity? The question of indicators has been around for some time OSM, with some instead advocating for a few single-species indicators. Other maintain that a holistic community-level approach is required, lest we miss anthropogenic changes to species outside of a small indicator list. Our analysis suggests that OS activities affect the whole mammal community, ultimately affecting mammalian diversity. The importance of anthropogenic features swamps out natural variability in explaining patterns of mammal diversity, in highly- and moderately disturbed landscapes. This argues for this whole-community approach to monitoring, which thanks to camera traps can be executed at no extra cost than single-species monitoring.

Finally, we explore the reliability of a future indicator for TBM mammals: animal density. Density is a Holy Grail for ecology, being a real biological property that changes with available resources and fluctuating environmental challenges. It is also one of the most difficult to obtain, especially from animals without unique markings. We explored a new class of models – Spatial Count models – in an experimental setup in the OSR and found that SC models performed well at recovering known changes in density over time.

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.

## 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 the 2021-2022 year, workplans were approved in June and the landscape unit (LU)-based sampling budget was funded at 66% of the requested amount. This allowed us to sample two of the four LU's proposed under the BADR design (Figure 1). We opted to monitor the high disturbance (LU3) and low disturbance (LU2) landscapes, to examine the widest range of oil sands stressors. Monitoring at Joint Environmental Monitoring (JEM) sites is reported separately by Alberta Biodiversity Monitoring Institute (ABMI).

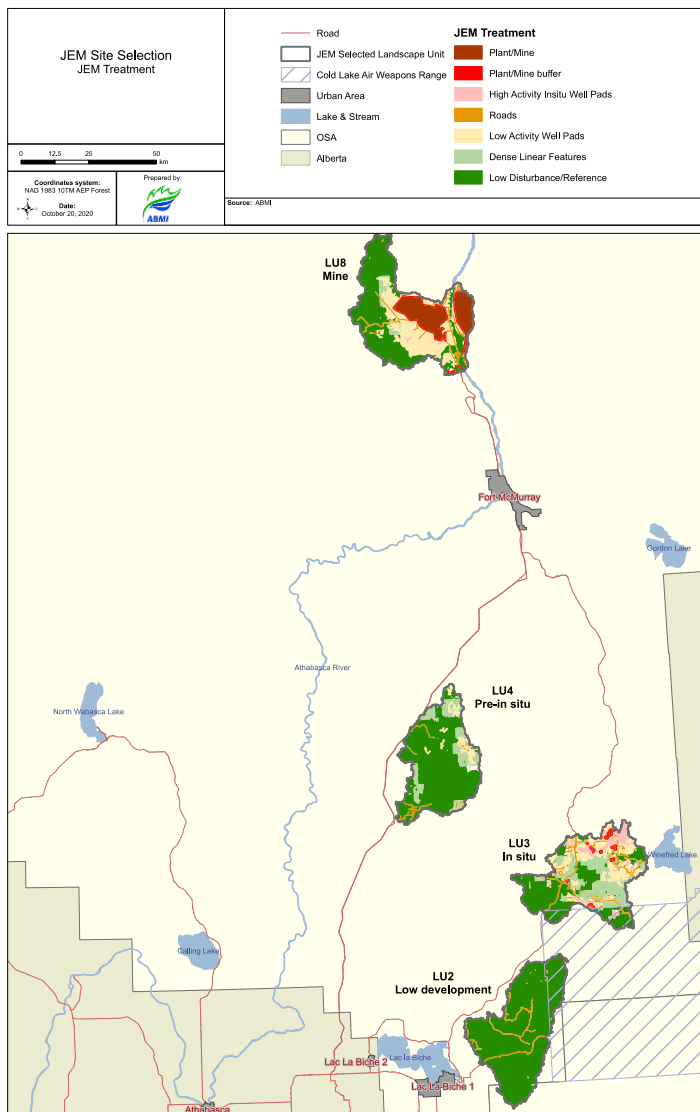


Figure 1. The TBM's BADR design with the four proposed LU's for 2021-2022. We monitored LU2 (low development) and LU3 (in situ).

## Sampling Design

For 2021 field work, 4 LUs were selected according to multiple criteria outlined in the BADR Technical Document. In addition to the JEM sites embedded in each LU, 50 cameras were deployed across each LU in a stratified random design we developed to minimise correlation among environmental covariates and spread sampling effort across the range of natural heterogeneity. The landscape was stratified into upland (>50% upland deciduous forest) and lowland (>50% wet coniferous forest) areas using the same 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-km<sup>2</sup> cells. This cell size allows us to space cameras sufficiently far apart to allow some degree of independence<sup>1-3</sup> for species-habitat models, typically conducted in a linear regression framework<sup>4-6</sup>. 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<sup>7-10</sup>. Using data from a review of mammal home ranges sizes<sup>11</sup> and analyses of caribou<sup>12</sup> and white-tailed deer<sup>13</sup> from the region, we determined the smallest home-range size was for white-tailed deer and that a 2-km<sup>2</sup> cell size would accommodate model requirements.

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 reduces expensive helicopter time. We then randomly selected 50 cells from each of the two 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 60 candidate sites (Figure 2a).

In the field, the deployment team visited the centroid of each cell and identified active wildlife trails suitable for deployment within that cell; this increases probability of detection given animal presence within the cell<sup>14-16</sup>, as data density is important to make statistical models function<sup>9</sup>. No bias is expected<sup>17</sup> 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 camera (Holmen, WI, USA) was deployed within the hex cell, close to the centroid but not necessary at the centroid. 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 inter-operability of datasets for different density estimation methods<sup>18,19</sup>. 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 2b).

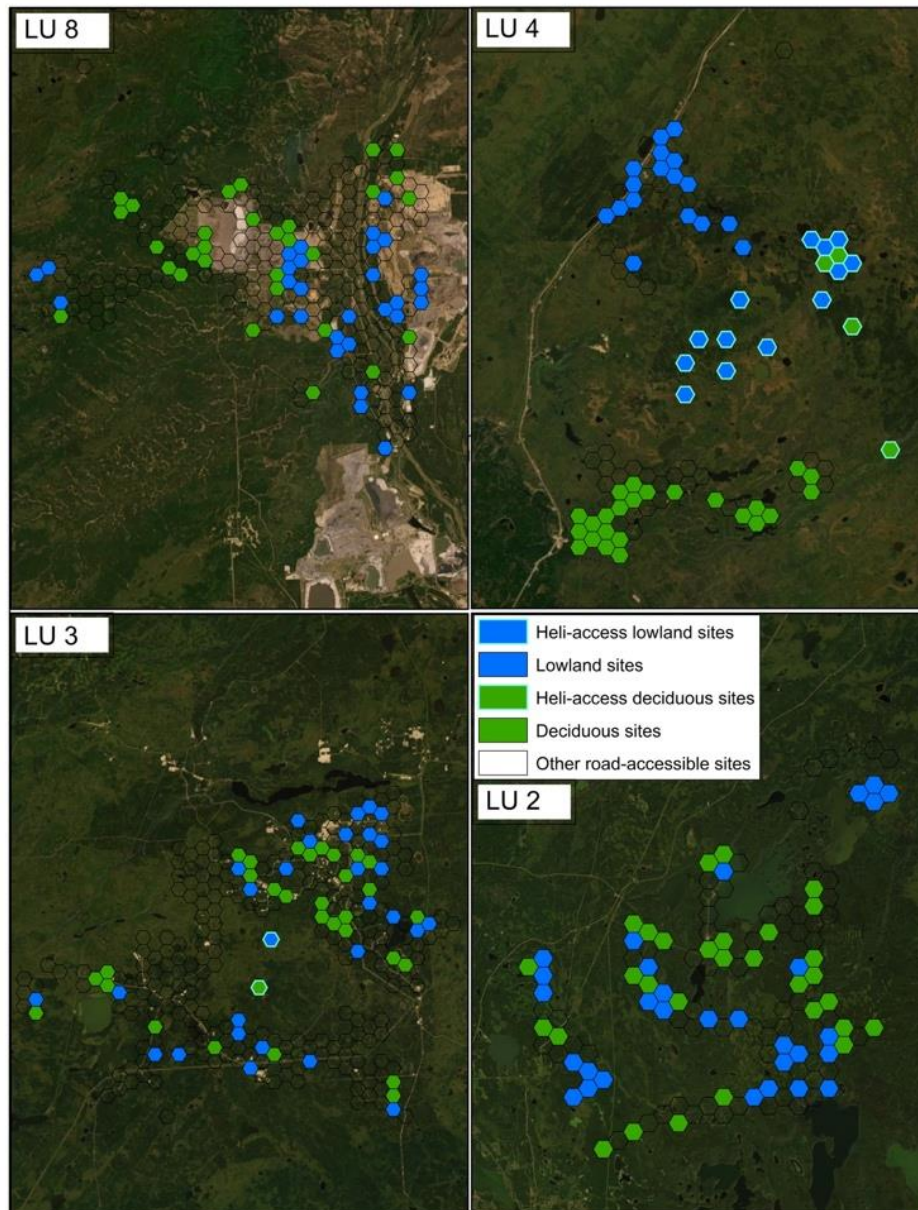


Figure 2a. The design criteria described herein generated these sampling arrays in each Landscape Unit (LU). The empty hexagonal cells represent all cells that met our constrained stratification criteria; the coloured cells are the random selection from this candidate set.

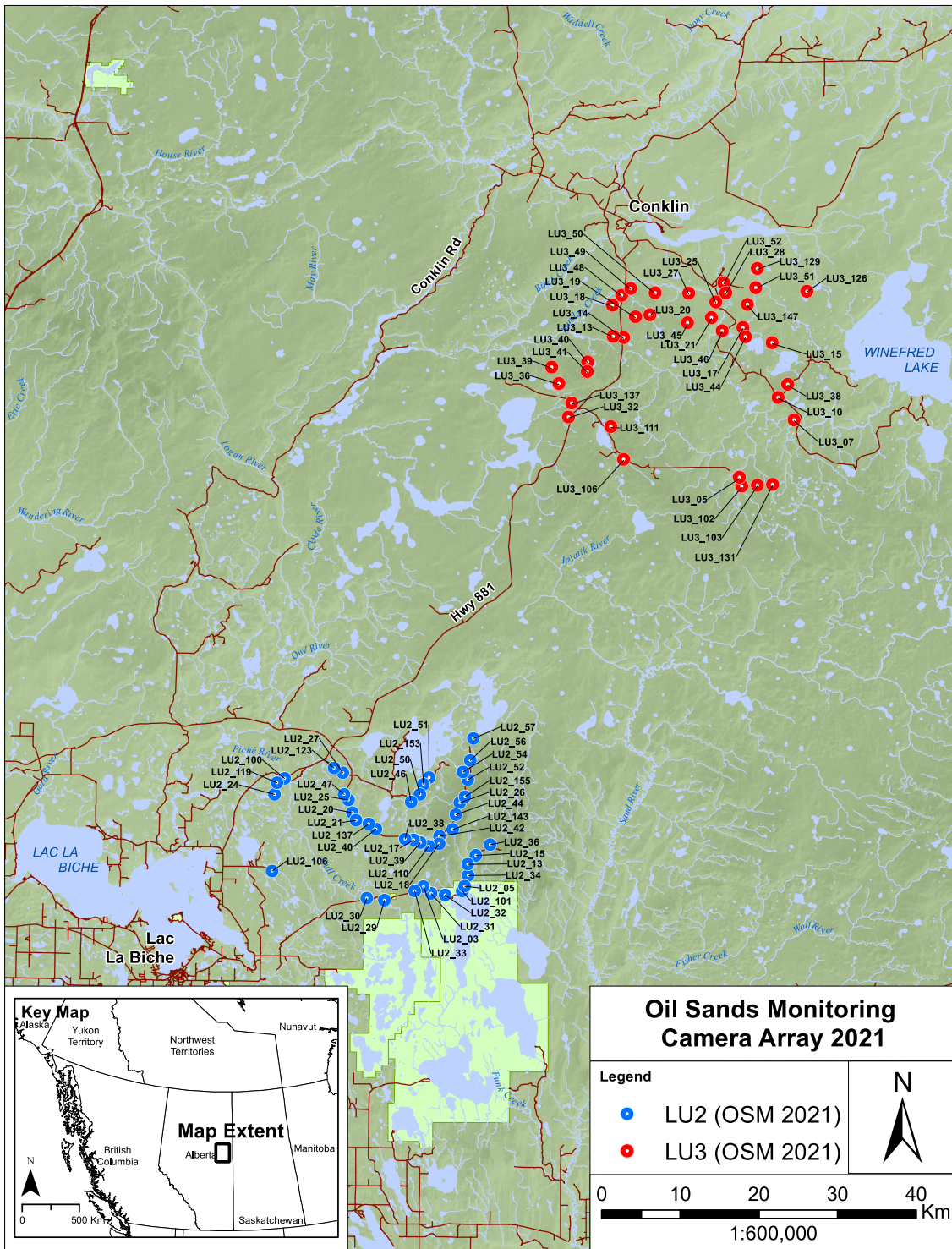


Figure 2b. The final sampling locations with LU2 and LU3; this is the outcome of dropping some candidate sites (Fig. 2a) that could not be feasibly and reliably accessed.

## Monitoring Results

Due to the late approvals, we could not deploy until July 2021; we desired at least a 6–7-month sample, as both the stressor-response and density estimation models require as many animal detections as possible, and these increase with time of sampling. We collected cameras in February 2022, but extremely deep snowpack and weather conditions prevented us from reaching all sites. Missing sites will be collected in spring 2022 following 2022-2023 workplan approvals. Here we collected 39 sites, and report on the detection frequencies of mammals, below.

### *LU2 Array*

Excluding unknowns, 21 different species were detected within the LU2 array. The top four most frequently detected species were White-tailed deer ( $n = 363$ ), Snowshoe hare ( $n = 300$ ), Black bear ( $n = 99$ ), and Coyote ( $n = 76$ ) (Figure 3A). The least frequently detected large mammals were Mule deer ( $n = 1$ ), Cougar ( $n = 2$ ), and Grey wolf ( $n = 3$ ). No humans (e.g., industrial workers, recreational users) apart from staff deploying and retrieving cameras were detected. White-tailed deer and Black bears were detected at 100% of sites in the LU2 Array, whereas Snowshoe hare and Coyotes were detected at 69% (Figure 3B).

### *LU3 Array*

Excluding unknowns, 18 different species were detected within the LU3 array. The top four most frequently detected species were White-tailed deer ( $n = 603$ ), Snowshoe hare ( $n = 155$ ), Black bear ( $n = 128$ ), and Coyote ( $n = 97$ ) (Figure 4A). The least frequently detected large mammals again included Mule deer ( $n = 1$ ), and Grey wolf ( $n = 1$ ), but no Cougars were detected in the LU3 array. Black bears were detected at 100% of sites in the LU3 Array, whereas White-tailed deer were detected at 96% of sites, Snowshoe hare and Coyotes at 83% (Figure 4B). Humans were detected at 22% of sites in the LU3 array.

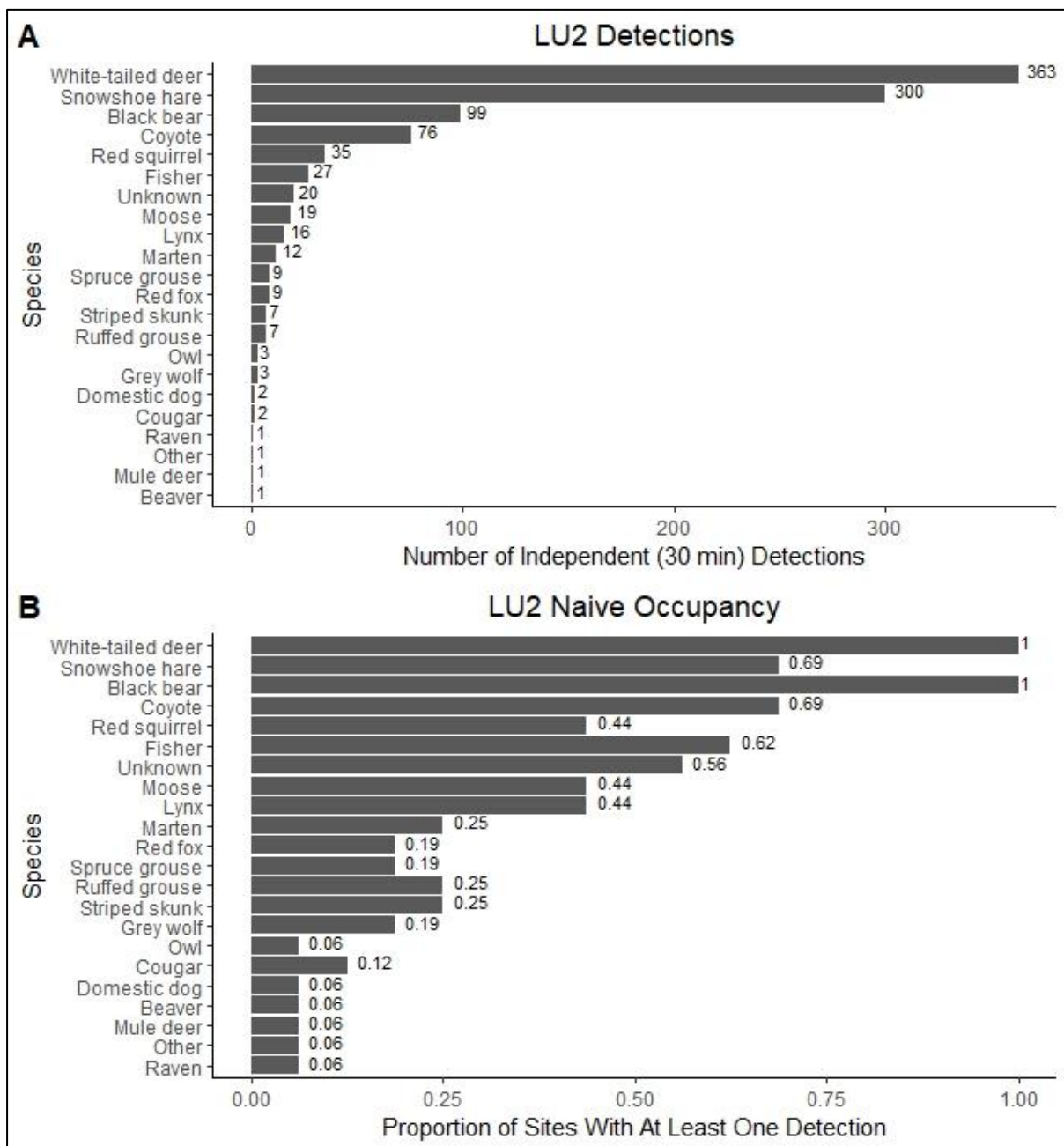


Figure 3. Summary results of A) independent detections and B) naïve occupancy from the LU2 array. Data sourced from 16 cameras deployed from July 2021 to February 2022.

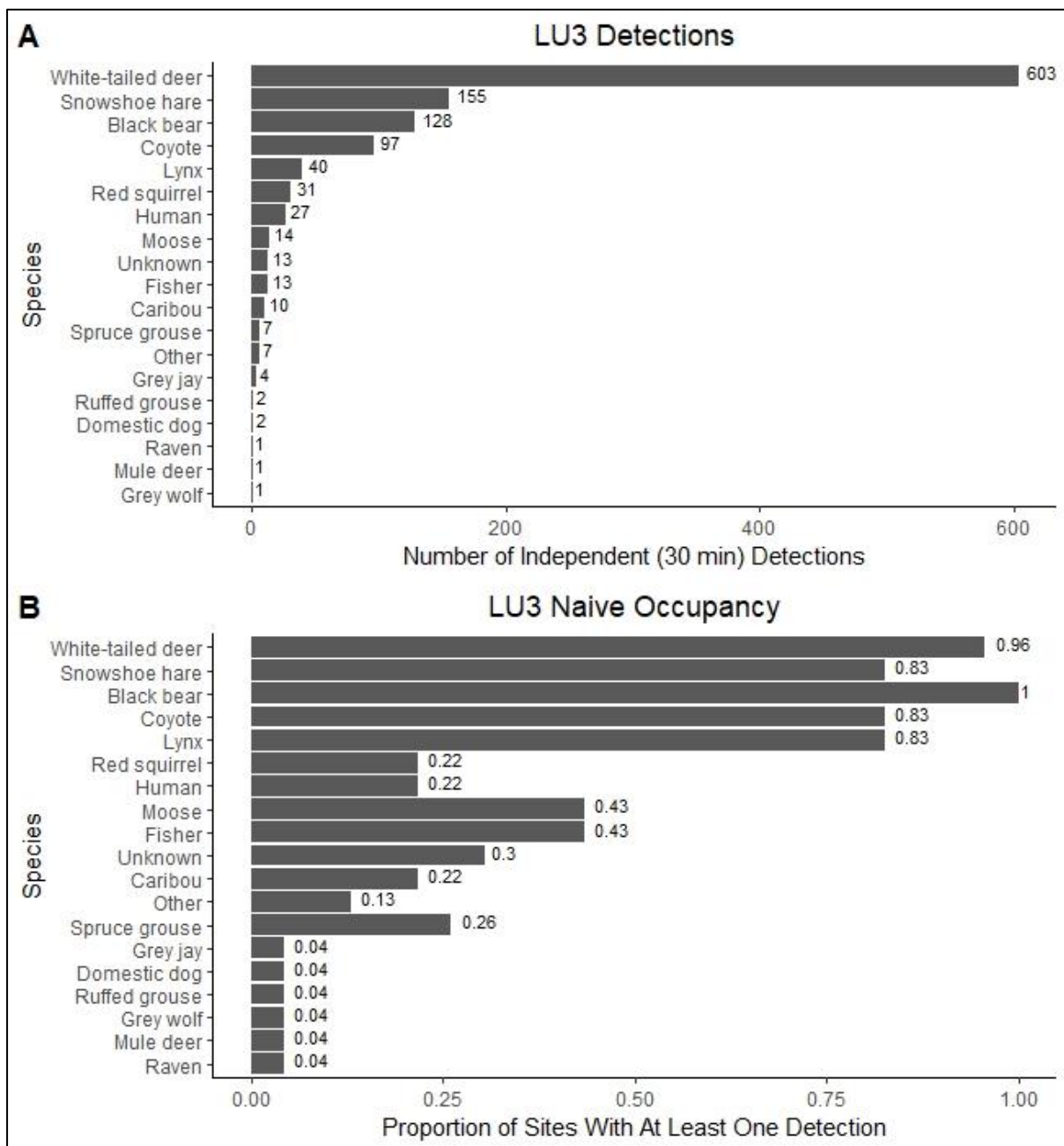


Figure 4. Summary results of A) independent detections and B) naïve occupancy from the LU3 array. Data sourced from 23 cameras deployed from July 2021 to February 2022.

### *Relative Abundance*

In the following Figures 5-20, for each array we plot the relative abundance for independent detections of Moose, White-tailed deer, Caribou, Grey wolves, Black bear, Coyote, Lynx and Snowshoe hare.

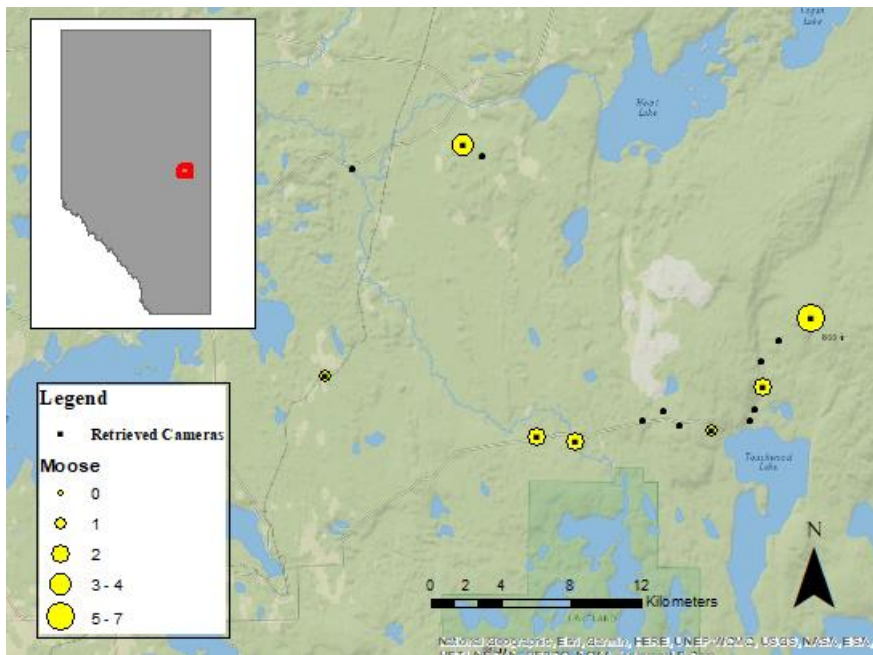


Figure 5. Number of independent detections of Moose from retrieved cameras in the LU2 Array

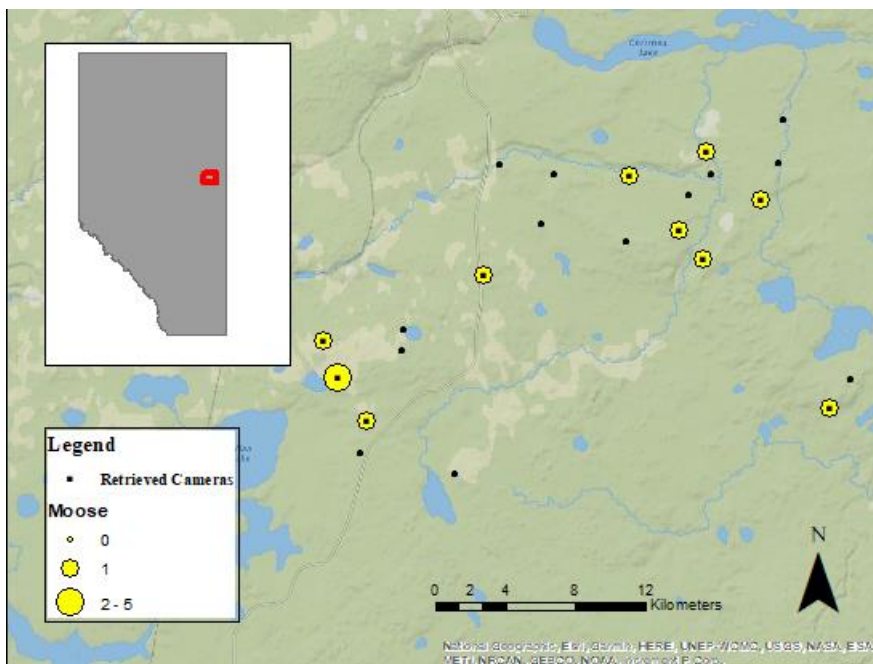


Figure 6. Number of independent detections of Moose from retrieved cameras in the LU3 Array

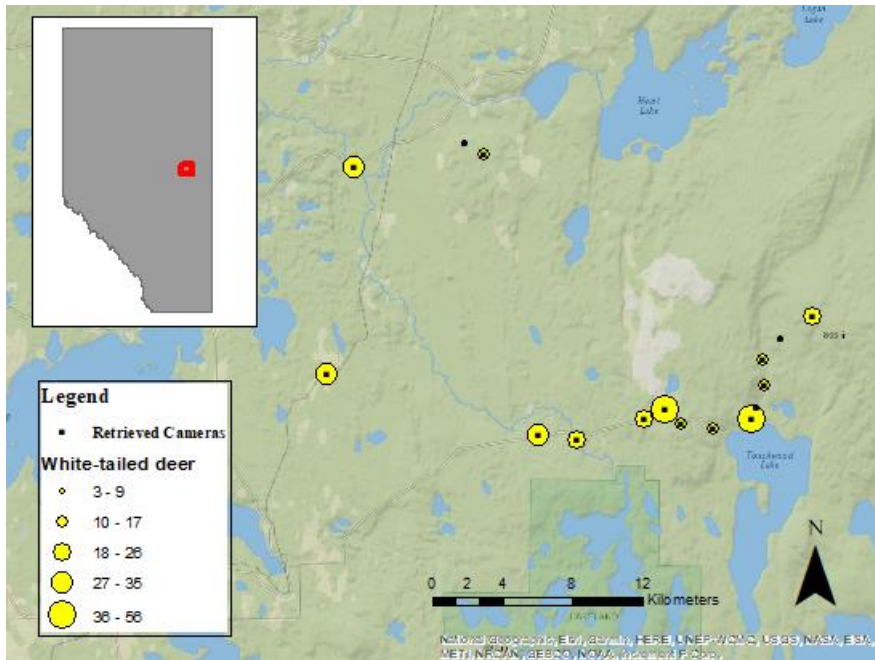


Figure 7. Number of independent detections of White-tailed deer from retrieved cameras in the LU2 Array

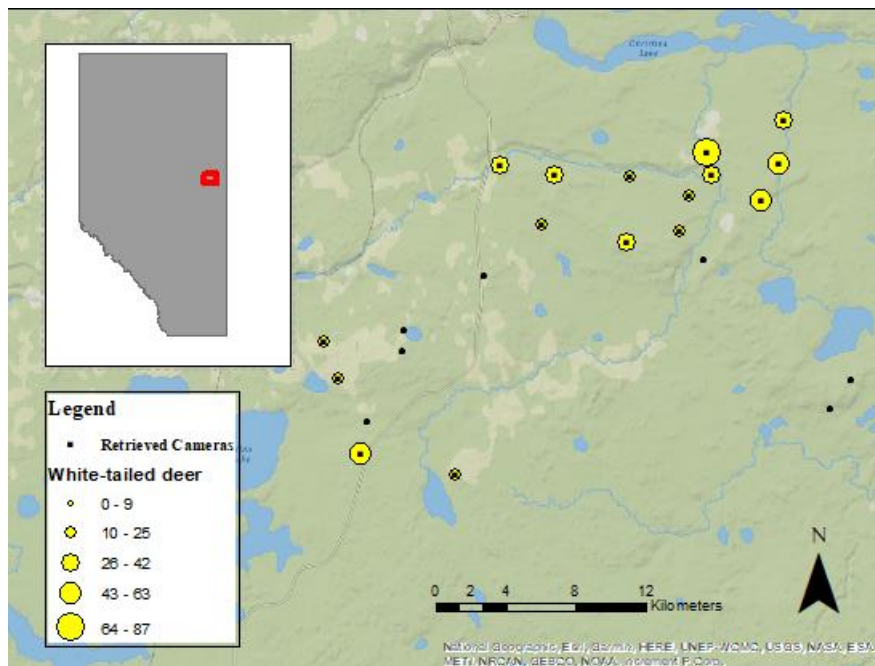


Figure 8. Number of independent detections of White-tailed deer from retrieved cameras in the LU3 Array

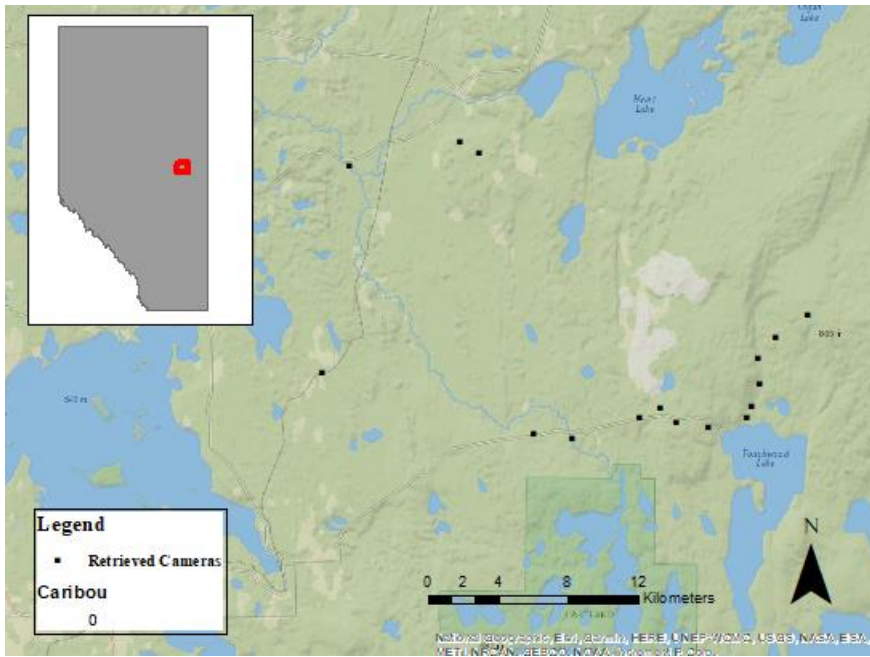


Figure 9. Number of independent detections of Caribou from retrieved cameras in the LU2 Array.

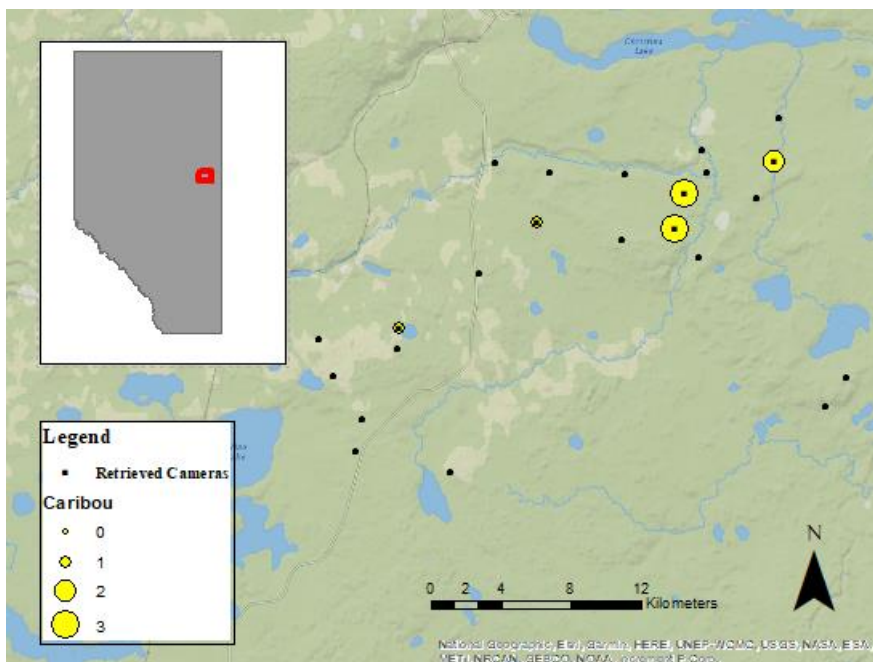


Figure 10. Number of independent detections of Caribou from retrieved cameras in the LU3 Array

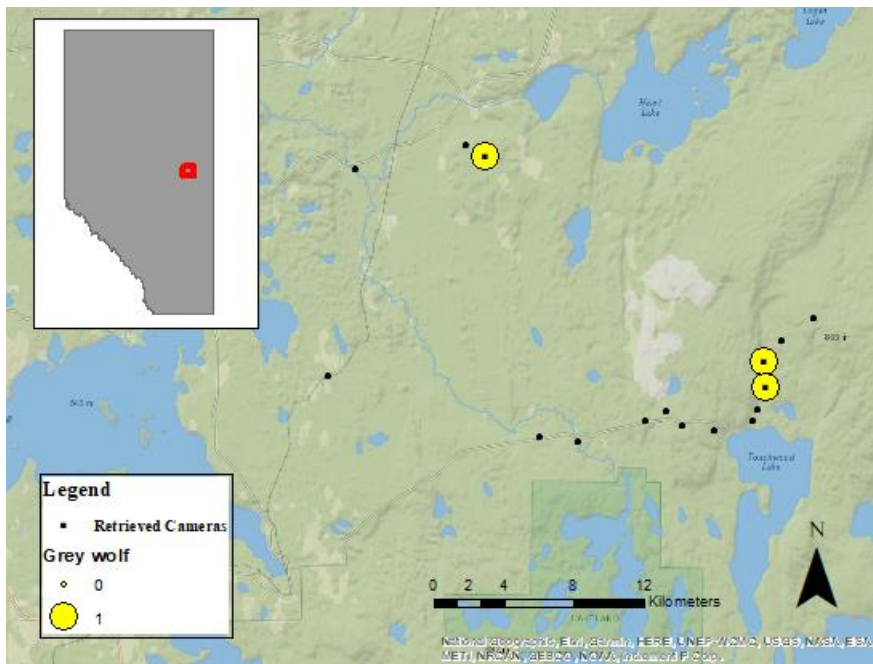


Figure 11. Number of independent detections of Grey Wolves from retrieved cameras in the LU2 Array

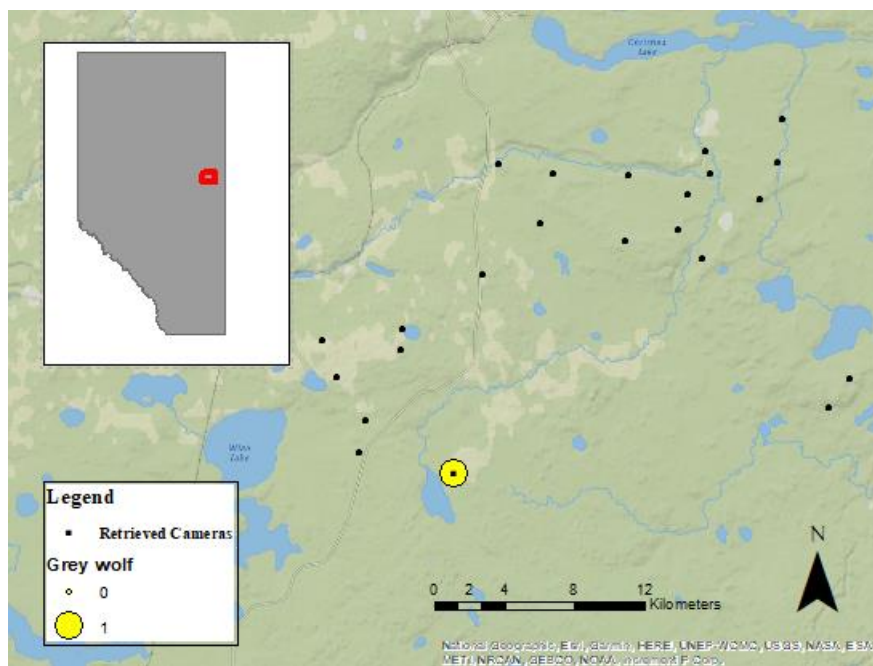


Figure 12. Number of independent detections of Grey wolves from retrieved cameras in the LU3 Array

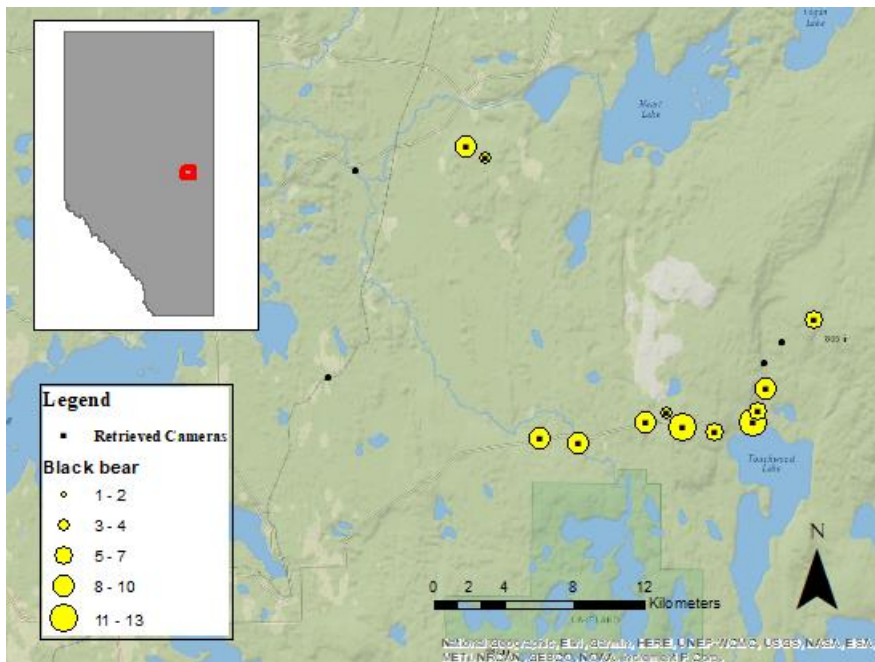


Figure 13 Number of independent detections of Black bears from retrieved cameras in the LU2 Array.

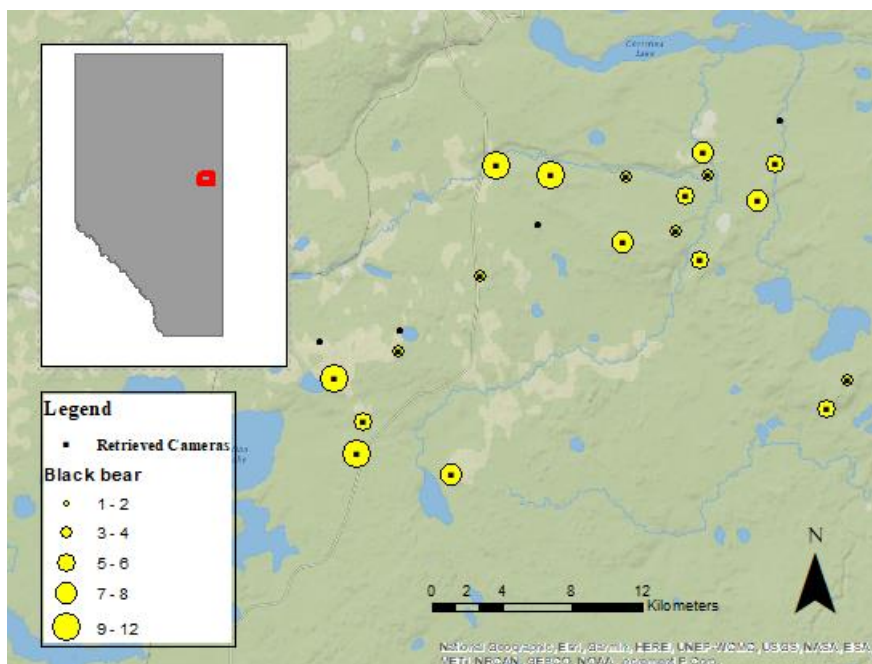


Figure 14. Number of independent detections of Black bears from retrieved cameras in the LU3 Array

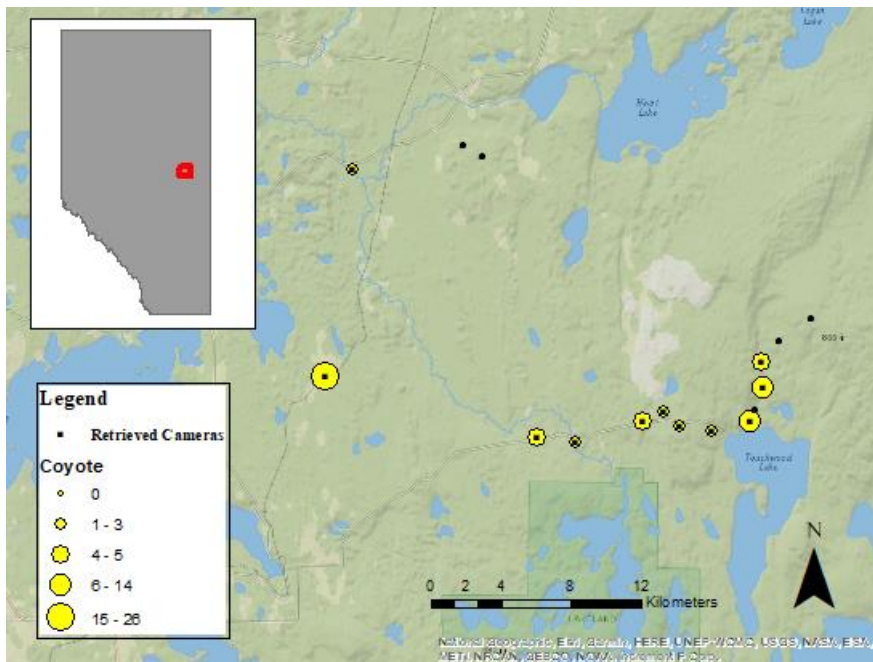


Figure 15. Number of independent detections of Coyotes from retrieved cameras in the LU2 Array

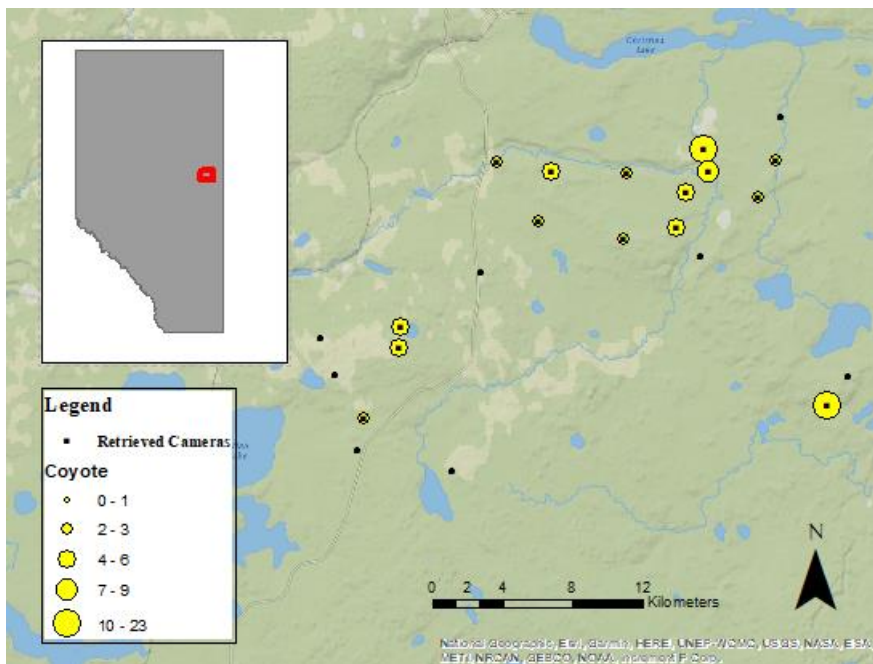


Figure 16. Number of independent detections of Coyotes from retrieved cameras in the LU3 Array

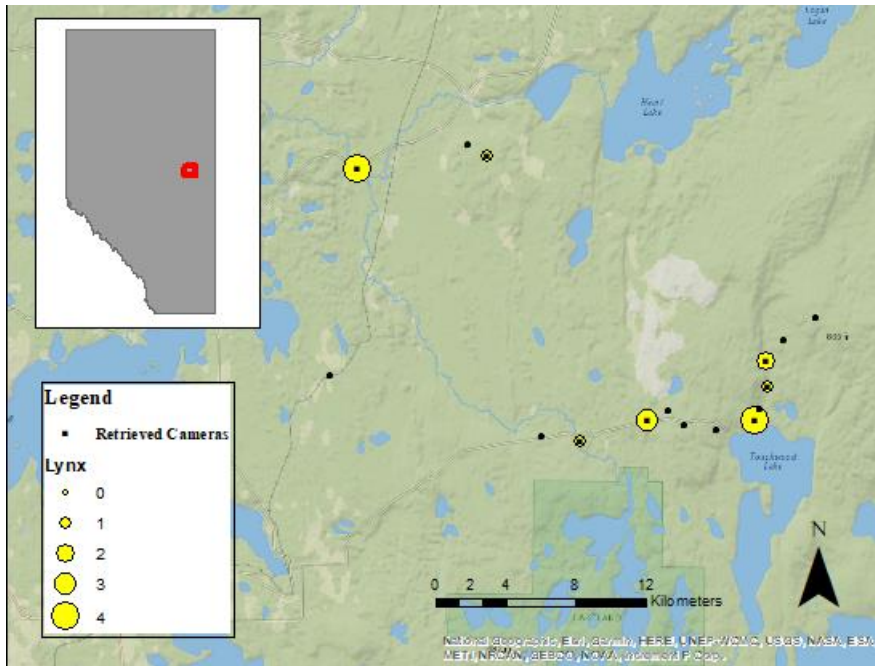


Figure 17. Number of independent detections of Lynx from retrieved cameras in the LU2 Array

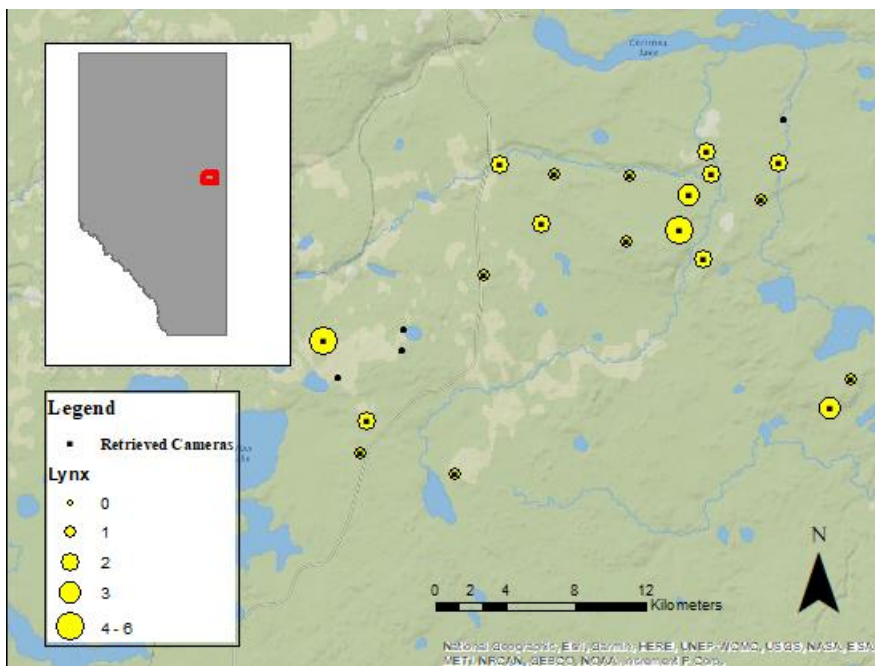


Figure 18. Number of independent detections of Lynx from retrieved cameras in the LU3 Array

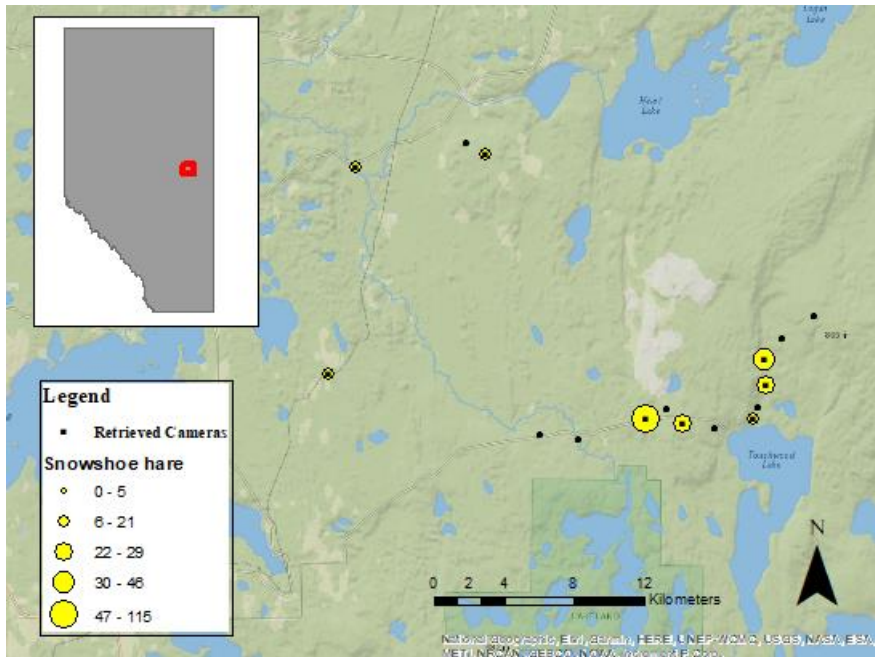


Figure 19. Number of independent detections of Snowshoe hares from retrieved cameras in the LU2 Array

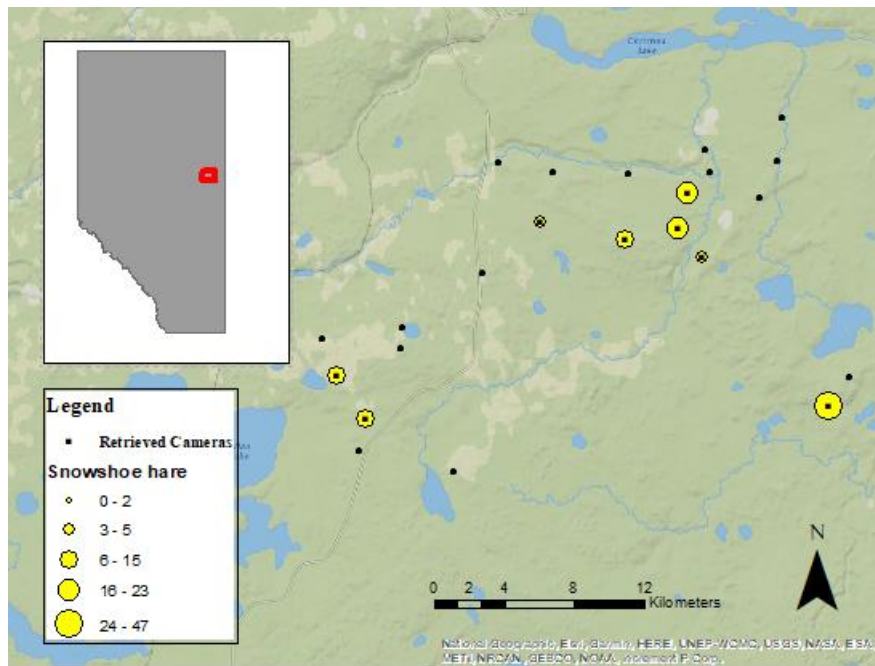


Figure 20. Number of independent detections of Snowshoe hares from retrieved cameras in the LU3 Array

## ACME Lab Public Data Portal

The ACME Lab's data portal lists maps and metadata for OSM TBM mammals monitoring: <http://www.acmelab.ca/osm.html>. This portal describes where and when monitoring has occurred. The links therein point to the University of Victoria's data repository: *Dataverse*. 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*<sup>20</sup> in CSV format.
5. Dataframes for R statistical software<sup>21</sup> that merge all the associated datasets and provide code for exploring the modelling the data.

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BOREAL LANDSCAPES - OIL SANDS MONITORING

Map showing Boreal Landscapes in Alberta, Canada. Landscape Type: Boreal.

DATA PORTAL

Data type: Camera data	Landscape: LU 2	Landscape: LU 3
Landscape: 2	Timespan: 2021-2022	Timespan: 2021-2022
Camera sites: 100	Camera data and models: Downloadable at Dataverse.	Camera data and models: Downloadable at Dataverse.
Area: 3500 km <sup>2</sup>	Landcover data: Downloadable at Dataverse, derived from the ABMI's <a href="#">Human Footprint Database</a> .	Landcover data: Downloadable at Dataverse, derived from the ABMI's <a href="#">Human Footprint Database</a> .
	Metadata: See Publications, below.	Metadata: See Publications, below.
	OSM ARRAY (LU2)	OSM ARRAY (LU3)

## CONTEXT-SPECIFIC CHANGES IN SPECIES-STRESSOR RELATIONSHIPS ACROSS THE BOREAL FOREST: UNDERSTANDING DRIVERS OF DIVERSITY

### **Preface for OSM: Adaptive Environmental Effects Monitoring**

The Oil Sands Monitoring Program has adopted adaptive EEM monitoring<sup>22-24</sup> as a paradigm for cost-effective monitoring. The specifics of how to apply adaptive monitoring EEM to the Terrestrial Biological Monitoring (TBM) program have yet to be revealed, as the traditional application to aquatic environments using statistical thresholds is not applicable here, where stressor-responses can vary widely across contexts and landscapes. 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. The question becomes, can we expect stressor-responses to be consistent among landscapes? This research starts to answer that question.

The implementation of BADR field sampling began only this 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 arrays<sup>25</sup>, each considered a coordinated distributed experiment<sup>26</sup> 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 measured mammalian species’ alpha diversity<sup>27-29</sup> – diversity at the camera trap. We modelled how species diversity relates to natural and anthropogenic features in each landscape. We predicted that the relation between disturbance and diversity would change among highly-, moderately-, and minimally disturbed landscapes.

This is precisely what we found: the relationship between a feature (like seismic lines) and diversity is *not consistent* among landscapes, but changes with the landscape context. Extrapolating stressor-response relationships from one area to another cannot be reliably done without some knowledge of the landscape context. What defines “context” is a question that ongoing monitoring and associated analyses under the BADR design, is designed to answer. One contextual factor is the degree of disturbance. Pivotaly, we also show that although “intactness” as measured by ABMI is around 90% in the OSR, the current footprint in high-disturbance landscapes footprint is sufficient to overwhelm natural landscape

processes as predictors of mammalian diversity – confirming the need for monitoring this key indicator taxa.

### **How can this knowledge be used for OSM?**

We show that highly disturbed *in-situ* landscapes on outsized effect on mammalian diversity, and we recommend that these be maintained as a focus for future monitoring should triaging be necessary. This does not mean we should abandon the BADR design's inclusion of moderate- and low-disturbance landscapes. Instead, it shows where focus can be directed as resources require it and emphasizes the importance of the effects of in-situ development on mammalian diversity. The total footprint may be smaller than mineable monitoring LUs, but the spatial distribution of the anthropogenic landscape features has an outsized effect. This knowledge helps guide selection of Landscape Units (LUs) for future years of the BADR-based TBM.

### **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. The previous systematic sampling conducted by ABMI, though strong for other analyses such as trends, was not designed to answer these questions. 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 LU's were 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 as the program unfolds.

This paper is drafted as a manuscript submission to *Global Ecology and Biogeography*.

**Authors:** Macgregor Aubertin-Young<sup>1,a</sup>, Andrew Ladle<sup>1</sup>, Joanna Burgar<sup>2</sup>, A. Cole Burton<sup>2</sup>, Nicole Heim<sup>3</sup>, Fabian Grey<sup>4</sup>, John Paczkowski<sup>5</sup>, Eric Higgs<sup>1</sup>, and Jason T. Fisher<sup>1</sup>

<sup>1</sup>*School of Environmental Studies, University of Victoria, 3800 Finnerty Road, Victoria, Canada. V8P 5C2*

<sup>2</sup>*Department of Forest Resources Management, University of British Columbia, 2424 Main Mall, Vancouver, BC, V6T 1Z4, Canada*

<sup>3</sup>*Ktuxana National Council*

<sup>4</sup>*Whitefish Lake First Nation. General Delivery, Atikameg, Alberta, Canada. T0G 0C0*

<sup>5</sup>*Government of Alberta*

## Introduction

Biodiversity is unevenly distributed because of complex interactions between organisms and their environment (Gaston, 2000). These interactions involve numerous factors, including historical, climatic, and physical features of the environment, although a small number of factors often outweigh others as dominant determinants of species diversity (Whittaker et al., 2001). Biogeography has largely centered on finding these dominant diversity determinants, especially at continental and global scales, which has exposed variability in their strength and identity across spatial scales (Field et al., 2009; Shmida & Wilson, 1985). At very fine spatial scales (i.e.,  $< 1 \text{ km}^2$ ; hereafter ‘local’), however, where species diversity has been most directly impacted by anthropogenic activities, the dominant determinants of species diversity remain unclear (Field et al., 2009).

Productivity, habitat heterogeneity, and keystone structures are among major hypothesized determinants of species diversity. The productivity hypothesis is perhaps the most prominent, positing that productivity limits the number of species than area can support (Waide et al., 1999). The similarly established habitat heterogeneity hypothesis posits that habitat heterogeneity increases resource diversity and thus niche space, allowing more species to coexist (Stein et al., 2014). The keystone structures hypothesis, in contrast, is lesser recognized; slightly modified from the original concept, it posits that specific “keystone structures” on the landscape increase species diversity by providing valuable, often limiting resources to multiple or keystone species (Tews et al., 2004). These hypotheses have each been variably supported at local scales (Field et al., 2009), but as major tenets of biogeography, they remain as potentially important determinants of local diversity.

In the era of global change, local diversity is noticeably shaped by both natural and anthropogenic features of the environment (Maxwell et al., 2016). This implies that productivity, natural habitat heterogeneity, and natural keystone structures, if important, now act alongside anthropogenic determinants of local diversity. Indeed, many studies have described anthropogenic diversity determinants in showing how anthropogenic activities, especially landscape changes, alter species diversity (Newbold et al., 2015; Wilson et al., 2016). Fewer studies, however, have directly compared the influence of anthropogenic diversity determinants to that of natural determinants (e.g., van Heezik et al., 2008), partially obscuring the ecological significance of anthropogenic determinants. This has maintained uncertainty in how strongly anthropogenic diversity determinants rival natural determinants, especially in relation to terrestrial mammal diversity. Mammals are highly sensitive to anthropogenic activities (Crooks et al., 2017) yet critical for ecosystem functioning (Lacher et

al., 2019), bringing their responses to anthropogenic activities to the forefront of conservation. In turn, we must compare how anthropogenic and natural factors shape local mammal diversity to fully weigh the ecological significance of anthropogenic pressures and reveal diversity-maintaining characteristics of the environment.

As many mammals move numerous kilometres in even a single day (Tucker et al., 2018), local mammal diversity describes the number of species using a relatively small patch of the landscape, as determined by species' movements and habitat use (hereafter "alpha diversity"). As such, alpha diversity likely reflects a dynamic subset of the regional species pool that may change as individuals traverse the landscape. Such fine-scale mammal diversity has been seldom studied relative to community and landscape-level (i.e., gamma) diversity (Field et al., 2009), even though ecological processes operating at very fine scales partly shape coarser diversity patterns (Huston, 1999) and majorly contribute to ecosystem functioning (Hooper et al., 2012). Understanding the determinants of alpha diversity may therefore reveal processes contributing to regional and global diversity distributions.

The northwest Nearctic is a valuable region in which to compare natural and anthropogenic determinants of mammalian alpha diversity, as forestry, mining, and fossil fuel extraction maintain vast networks of anthropogenic landscape features alongside natural habitats (Pickell et al., 2015). Among the most prominent anthropogenic features here are linear and polygonal forest clearings (Venier et al., 2014), which distinctly fragment and remove natural habitats with the potential to repel numerous mammal species (Fisher & Burton, 2018) and thus decrease alpha diversity. However, anthropogenic forest clearings have also been found to attract and benefit certain mammal species by providing anthropogenic resource subsidies (Fisher & Burton, 2018). Pipeline corridors and petroleum-exploration seismic lines (Dabros et al., 2018), for example, provide linear corridors along which species can travel faster (Dickie et al., 2017) and predators can more frequently encounter and thus predate upon prey (McKenzie et al., 2012). Likewise, petroleum-extraction well sites and forestry cutblocks (Fisher & Wilkinson, 2005) provide early seral vegetation on which herbivores and omnivores can forage (Serrouya et al., 2021). Recalling the habitat heterogeneity and keystone structures hypotheses, industrial landscape changes that introduce such forest clearings may therefore increase mammalian alpha diversity by introducing novel, anthropogenic keystone structures or contributing to habitat heterogeneity.

My objectives were two-fold. First, we compared how well the proportional coverage (hereafter 'proportion') and heterogeneity of anthropogenic forest clearings explained

mammalian alpha diversity—measured at the level of individual camera traps—relative to productivity, natural habitat heterogeneity, and potential natural keystone structures. I hypothesized that anthropogenic diversity determinants more strongly shape alpha diversity in more industrialized landscapes, although we did not predict which of the mechanisms (proportion or heterogeneity) would dominate. Second, we tested whether the proportions and heterogeneity of anthropogenic forest clearings increase mammalian alpha diversity, as predicted by the habitat heterogeneity and keystone structure hypotheses.

## 2. Methods

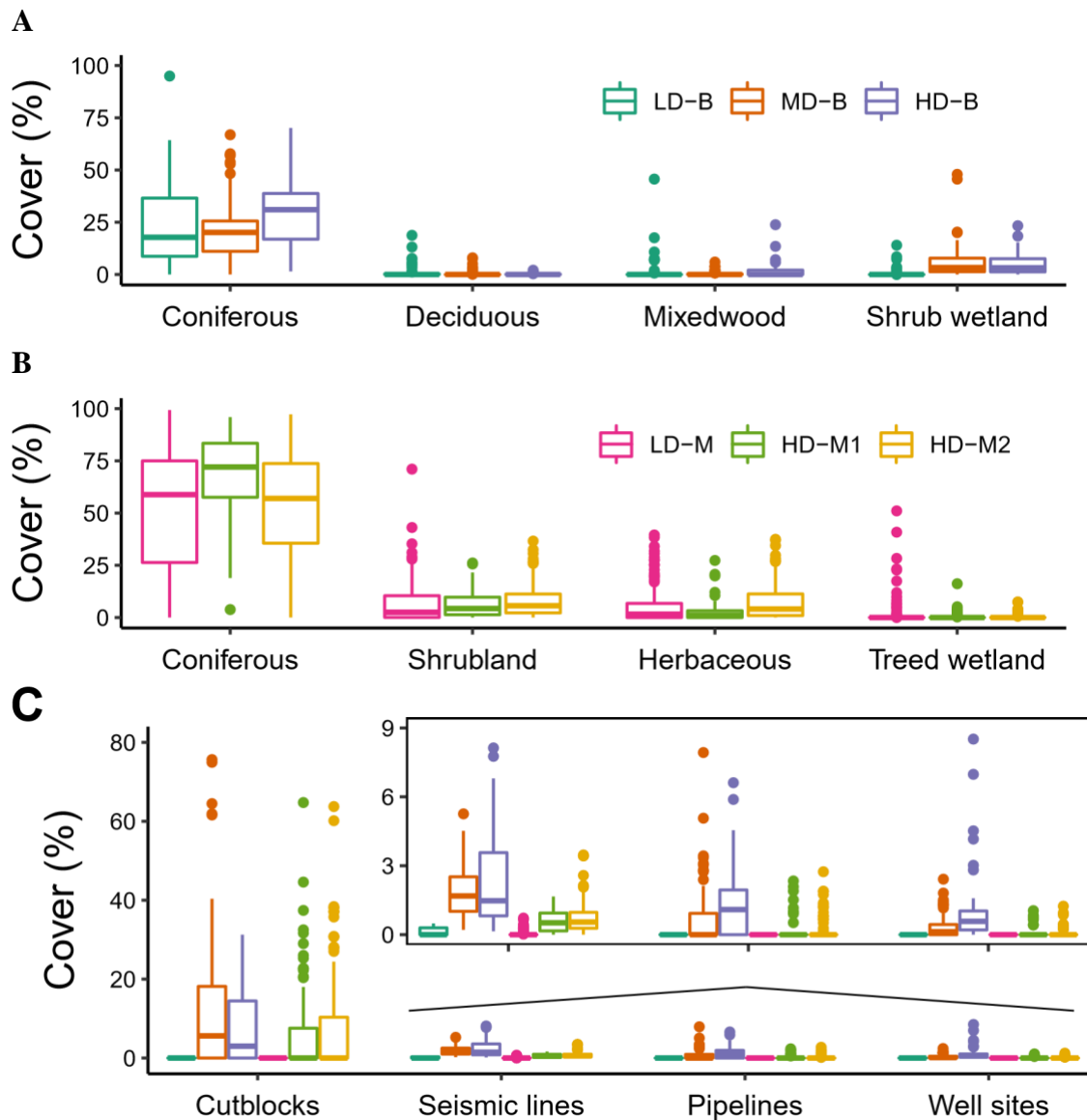
### 2.1. Study regions

We synthesized data from six distinct research landscapes in Alberta, Canada (Figure 2.1). Three of these landscapes span an anthropogenic disturbance gradient along the eastern slopes of the Canadian Rocky Mountains, containing similar natural environments of predominantly Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and subalpine larch (*Larix lyalli*) forests but variable proportions of anthropogenic features (Figure 2.2). Two of these three mountain landscapes—Kananaskis Country (Heim et al., 2019) and Bighorn Backcountry—are comparably disturbed by resource extraction and human recreation, evident in their near-equal proportions of seismic lines, pipelines, cutblocks, and well sites. The other mountain landscape—Willmore Wilderness (Fisher et al., 2011)—is largely protected from resource extraction and most forms of recreation; access is limited to foot and horseback riding trails. We hereafter refer to the lowly anthropogenically disturbed mountain landscape as “LD-M” and highly anthropogenically disturbed mountain landscapes as “HD-M1” (Bighorn Backcountry) and “HD-M2” (Kananaskis Country), abbreviating their degree of anthropogenic disturbance as low or high and environment as montane.

Three other landscapes—Christina Lake (Fisher & Burton, 2018), Whitefish Lake (Fisher et al., 2021), and Richardson Backcountry—span an anthropogenic disturbance gradient in the boreal forest, northeast of the mountains. These landscapes are naturally composed of white spruce (*Picea glauca*), black spruce (*Picea mariana*), and aspen (*Populus tremuloides*) forests, juxtaposed by peat-dominated wetlands. Christina Lake, hereafter ‘HD-B’, has the highest proportion of seismic lines, pipelines, and well sites in the region (Pickell et al., 2015). Whitefish Lake, hereafter ‘MD-B’, has these same industrial features but at lower proportions. Conversely, Richardson Backcountry, hereafter ‘LD-B’, has very few anthropogenic features and limited human access. LD-B, however, was substantially

disturbed from fire several years before our study began. Note that we ranked the degree of anthropogenic disturbance separately between ecoregions, as equal proportions of anthropogenic features may have differing impacts on species diversity between distinct ecoregions (Allan et al., 2019).

The mammal communities are similar among landscapes, though more speciose in the mountains (Table A1). Species' functional groups include herbivores, omnivores, predators and scavengers, and prominent clades include ungulates, felids, canids, and mustelids (Krebs et al., 2001). Some communities also contain at-risk species, most notably endangered woodland caribou (*Rangifer tarandus caribou*).



**Figure 2.1.** Boxplots of the proportional coverage of natural (A–B) and anthropogenic (C) landcover classes in six variably industrialized landscapes in the northwest Nearctic. The proportional coverage of each class was measured within 1 km of camera traps that were deployed across each landscape; each point represents a different camera site. Figures A and B show natural habitats in boreal and mountain landscapes, respectively, and different colors represent different landscapes.

**Table 2.1.** Candidate model covariates used to explain mammalian alpha diversity in northwest Nearctic landscapes. (B) and (M) indicate natural keystone structure covariates used in boreal and mountain landscapes, respectively. Data were obtained from the Alberta Vegetation Index and the Alberta Biodiversity Monitoring Institute Human Footprint Map

Hypothesis	Model covariates (+ (1 Site))
Anthropogenic heterogeneity	Anthropogenic heterogeneity*Season
Anthropogenic keystone structures	(Seismic + Pipeline + Cutblock + Well)*Season
Natural heterogeneity	Habitat heterogeneity*Season
Natural keystone structures (B)	(Conifer + Decid + Mixedwood + Wetland)*Season
Natural keystone structures (M)	(Conifer + Shrub + Herb + Wetland)*Season
Null	Season
Productivity	EVI*Season

## 2.2. Sampling designs

We synthesized data from motion-activated camera traps (models RM30, PM30, PC900, HPF2X; Reconyx, Holmen, WI) that were deployed in each landscape using probabilistic sampling designs, the specifics of which varied due to logistical constraints and variable landscape structures (Table A2). As landscapes were sampled by different schedules and with the possibility of camera malfunctions, we only included cameras that were active during our study periods (January–March or July–September) and had at least one animal detection. For each site in each landscape, a single camera was placed along a game trail to increase the probability of detecting an animal given presence, and cameras were separated by an average minimum distance of 4.0 km (standard deviation = 2.2 km) to minimize spatial autocorrelation. We describe the specific sampling designs for each landscape in Table A2.

## 2.3. Alpha diversity measurements

In each landscape, we calculated alpha diversity at individual camera sites (i.e., localities) by estimating the asymptotic species richness from species' site-level relative abundances, which we performed with the R package *iNEXT* (Hsieh et al., 2020). This was based on the Chao1 estimator, which provides a lower bound estimate of alpha diversity using the number of observed and rare species in the sample (Colwell & Coddington, 1994). We estimated alpha diversity using the Chao1 estimator because each camera likely provides

only a sample of individuals present at each site (Kays et al., 2021), implying that observed alpha diversity may underestimate true alpha diversity. We also used the Chao1 estimator to control for variability in the number of camera images captured (analogous to individuals sampled) between sites, recognizing that larger samples will likely be more diverse as a sampling artifact (Colwell & Coddington, 1994). We measured species' site-level relative abundance as the number of independent images of each species at each site, and we considered images of the same species to be independent if they were taken more than 1 hour apart.

We took repeat measures of alpha diversity using three consecutive 30-day sampling periods during summer (July–September) and winter (January–March), yielding three alpha diversity estimates per site per season. For landscapes LD-M and HD-M, however, we used two consecutive 30-day periods because of their shorter sampling durations. We took repeat measures to capture month-long ‘snapshots’ of alpha diversity within each landscape, as animal movements between localities may cause temporal variation in alpha diversity that we intended to capture. We did not sample for fewer than 30 days to allow for rare species to be detected, which may require numerous days (Kays et al., 2020). We included all observed mammal species except bats and domestic livestock. Note that we did not compare gamma diversity between landscapes because landscapes varied in size and were sampled using different designs, allowing for potentially spurious conclusions that reflect species–area relationships (Scheiner et al., 2000) and unequal species detection probabilities (Hofmeester et al., 2019) rather than biogeographic patterns.

#### *2.4. Natural and anthropogenic diversity determinants*

We used satellite-derived landcover datasets to measure productivity and the proportion and heterogeneity of natural and anthropogenic landscape features within a circular buffer around each camera site. To consider possible scale–dependence in how these landscape features affect alpha diversity (Fisher et al., 2011), we measured each feature using buffer radii of 250–2500m in 250m increments. We measured productivity using the mean Enhanced Vegetation Index (EVI), a continuous measure of vegetation-reflected light intensity commonly used as a proxy for primary productivity (Sims et al., 2006). We obtained MODIS-derived EVI values at 250m resolution using the R package *MODISTools* (Tuck et al., 2014), and following recommendations to improve data quality, we removed EVI values less than 0 (suggestive of cloud interference) and greater than 0.9 (suggestive of dark surfaces, such as water; Boriah et al., 2010). As EVI is measured on 16-day intervals, we

averaged the two EVI values per site per 30-day sampling period. If EVI data were not available at a site for a particular sampling period, we used the averaged EVI value from the previous period. To reduce collinearity between EVI and season, we standardized EVI within seasons separately (mean = 0, standard deviation = 1) such that EVI values represent the difference from the relevant seasonal mean.

As we wanted to compare natural and anthropogenic diversity determinants and test whether the proportions of anthropogenic features increased alpha diversity, we measured the proportions of four anthropogenic features and four natural habitats that we refer to as potential keystone structures. To consider the most probable potential keystone structures, we chose anthropogenic features and natural habitats known to be used by multiple species or likely to benefit multiple species according to published literature (Bowman et al., 2010; Fisher & Burton, 2018; McKenzie et al., 2012). Accordingly, we considered the most prominent anthropogenic forest clearings as potential anthropogenic keystone structures: seismic lines, pipelines, cutblocks, and well sites. While seismic lines and pipelines are both linear clearings numerous kilometres long, seismic lines are often narrower and more densely distributed as a grid (Dabros et al., 2018). Likewise, cutblocks and well sites are both polygonal clearings, but cutblocks are often much larger (Brandt et al., 2013). We measured the proportion of anthropogenic features using the Alberta Biodiversity Monitoring Institute Human Footprint Map (Alberta Biodiversity Monitoring Institute, n.d.) from the year nearest available to the sampling year in each landscape.

For natural keystone structures, we considered different habitats between the distinct mountain and boreal ecoregions. In boreal landscapes, we considered lowland spruce forest, lowland deciduous forest, lowland mixedwood forest, and shrub wetland, which we reclassified from the Alberta Vegetation Inventory (Nesby, 1997). In mountain landscapes, we considered coniferous forest, shrubland, herbaceous, and treed wetland, which we reclassified using a 16-class landcover dataset (Nijland et al., 2015; Supplementary Information Table S3). We used separate landcover datasets between mountain and boreal landscapes because these datasets were classified with more detail than alternative datasets spanning all six landscapes. As with the anthropogenic landcover data, we measured the coverage of these habitats from the year nearest available to the sampling year in each landscape.

We measured the heterogeneity of anthropogenic features and natural habitats using Simpson's diversity index on the proportions of potential anthropogenic and natural keystone structures, respectively (*sensu* Katayama et al., 2014). To enable appropriate use of the index,

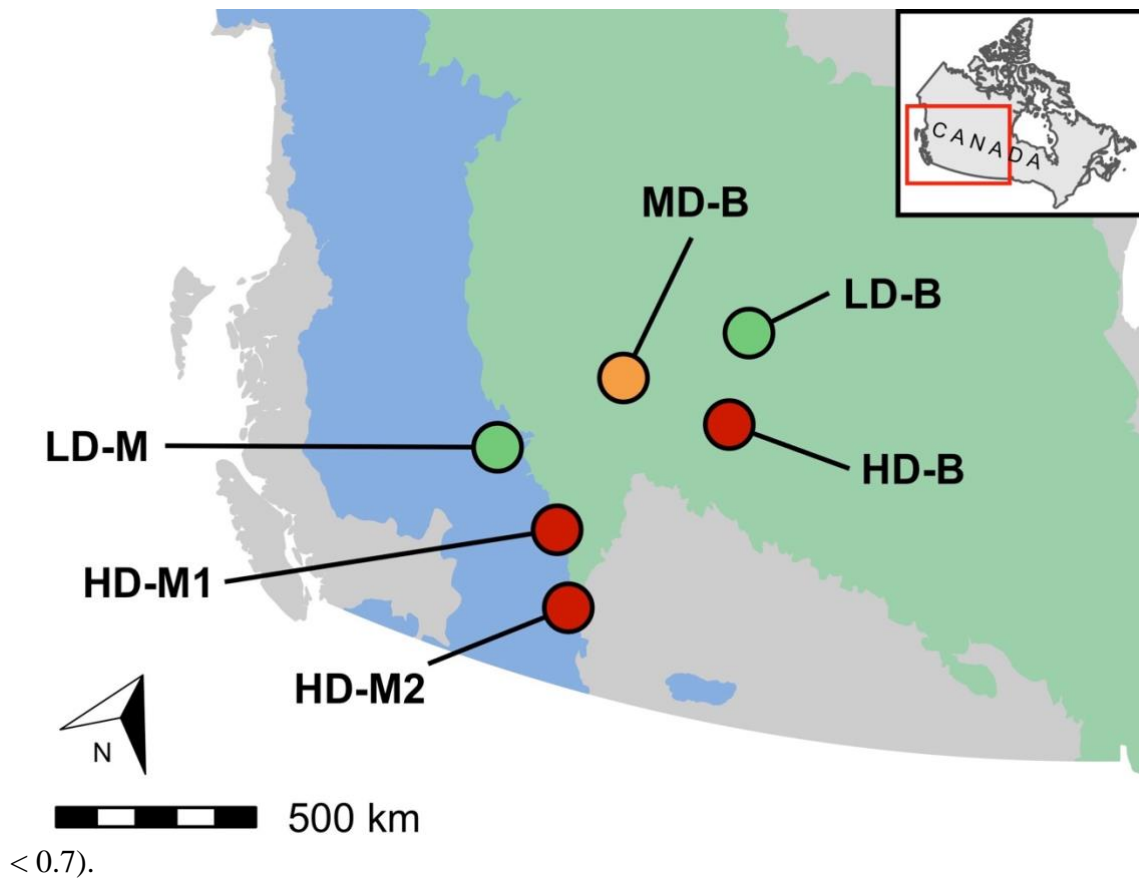
we first scaled the total proportional cover of the four potential natural or anthropogenic keystone structures to 1. This heterogeneity measure therefore describes the heterogeneity of adjacent landscape features irrespective of their absolute cover.

### *2.5 Modelling: Spatial scale and model selection*

We created five candidate models that each corresponded to a hypothesized determinant of alpha diversity: productivity, natural or anthropogenic landscape heterogeneity, or natural or anthropogenic keystone structures (Table 2.1). Productivity and both landscape heterogeneity models were represented by a single covariate (EVI and Simpson's diversity index, respectively) while both keystone structure models were represented by four covariates (the proportion of each potential anthropogenic or natural keystone structure). To compare the maximum support for each of these models in each landscape, we first found the best-supported spatial scale at which each covariate explained mammalian alpha diversity in each landscape. To do this, we separately regressed alpha diversity against each covariate at each spatial scale (250–2500m) using generalized linear mixed-effects models with a log-link and zero-inflated Gamma distribution, implemented with the R package *glmmTMB* (Brooks et al., 2017). We included season and season–covariate interactions as fixed predictors in each of these models to account for potential season-dependent relationships (Schooley 1994), and we included camera site as a random intercept to account for repeated alpha diversity measurements at each camera (Zuur et al., 2009). We used summer as the reference level for interaction terms. We then ranked the models for each covariate in an information-theoretic framework (Burnham and Anderson 2002) to determine the best-supported scale, based on which scale had the lowest sample size-corrected Akaike Information Criterion (hereafter 'AIC'; sensu Fisher et al., 2011).

Next, we used model selection to compare how well each model (i.e., diversity determinant, at the best-supported spatial scale) explained alpha diversity in each landscape. We could not compare anthropogenic diversity determinants in the lowly anthropogenically disturbed landscapes (LD-M and LD-B) because the proportions of anthropogenic features were too low for model convergence, leaving comparisons between only the natural determinants. In this step, we included a sixth model with season as the only fixed predictor and site as a random intercept, thereby comparing support for each determinant against a “null” model. We considered models with  $< 2 \Delta AIC$  to have the highest support, and we used 10-fold cross-validation to assess model fit (Roberts et al., 2017). While interpreting these models, we considered  $\beta$  estimates to be significantly different from zero if the 95%

confidence interval did not overlap zero. We standardized model covariates (mean = 0, standard deviation = 1) within each landscape and ensured that none were highly collinear ( $r$



**Figure 2.2.** Northwest Nearctic landscapes in which camera traps were deployed to compare hypothesized determinants of mammalian alpha diversity. Landscapes are in the montane cordillera (blue) and boreal (dark green) ecoregions and have low (green circles), medium (orange), or high (red) levels of anthropogenic disturbance from industrial resource extraction.

## Results

### *2.1. Anthropogenic diversity determinants outweighed natural determinants in highly industrialized landscapes*

Anthropogenic landscape features explained mammalian alpha diversity better than productivity, habitat heterogeneity, and natural keystone structures in each highly anthropogenically disturbed landscape (Tables 2.2–2.3). Of these three landscapes, the coverage of potential anthropogenic keystone structures explained alpha diversity better than anthropogenic heterogeneity in two (HD-M1:  $AIC_w = 0.76$ ; HD-B:  $AIC_w = 0.98$ ). In the other, anthropogenic heterogeneity best explained alpha diversity (HD-M2:  $AIC_w = 0.82$ ). In contrast, natural keystone structures best explained alpha diversity in the moderately anthropogenically disturbed boreal landscape, and neither the coverage of potential anthropogenic keystone structures ( $AIC_w = 0.00$ ) nor anthropogenic heterogeneity ( $AIC_w = 0.01$ ) explained alpha diversity better than the null model ( $AIC_w = 0.01$ ). Productivity and natural habitat heterogeneity variably explained alpha diversity across each of these four anthropogenically disturbed landscapes.

### *2.1. Anthropogenic features had variable effects on alpha diversity*

The proportion of potential anthropogenic keystone structures had variable effects on alpha diversity (Figure 2.3). Alpha diversity only increased with the proportion of well sites, which occurred in all highly anthropogenically disturbed landscapes, irrespective of ecoregion (HD-M1:  $\beta_{\text{Well}} = -0.56 \pm 0.47$ ,  $p = 0.020$ ; HD-M2:  $\beta_{\text{Well}} = 0.50 \pm 0.35$ ,  $p = 0.004$ ; HD-B:  $\beta_{\text{Well}} = 0.12 \pm 0.09$ ,  $p = 0.005$ ). However, alpha diversity did not change with the coverage of well sites in the moderately anthropogenically disturbed boreal landscape (MD-B:  $\beta_{\text{Well}} = 0.14 \pm 0.22$ ,  $p = 0.207$ ). The relationship between the proportion of well sites and alpha diversity did not change between seasons in three of four anthropogenically modified landscapes (HD-M1:  $\beta_{\text{Well:Seas}} = 0.19 \pm 0.47$ ,  $p = 0.425$ ; MD-B:  $\beta_{\text{Well:Seas}} = 0.20 \pm 0.38$ ,  $p = 0.303$ ; HD-B:  $\beta_{\text{Well:Seas}} = -0.06 \pm 0.11$ ,  $p = 0.257$ ) but weakened in winter in the other (HD-M2:  $\beta_{\text{Well:Seas}} = -0.60 \pm 0.39$ ,  $p = 0.002$ ).

**Table 2.2.** AICc tables of generalized linear mixed-effects models used to explain mammalian alpha diversity in mountain landscapes (LS) using different hypotheses. The covariates associated with each hypothesis are described in Table 2.1.  $k$  is the number of covariates; AICc<sub>w</sub> is the AICc weight. LL is the log-likelihood. RMSE is the root mean squared error using 10-fold cross-validation.

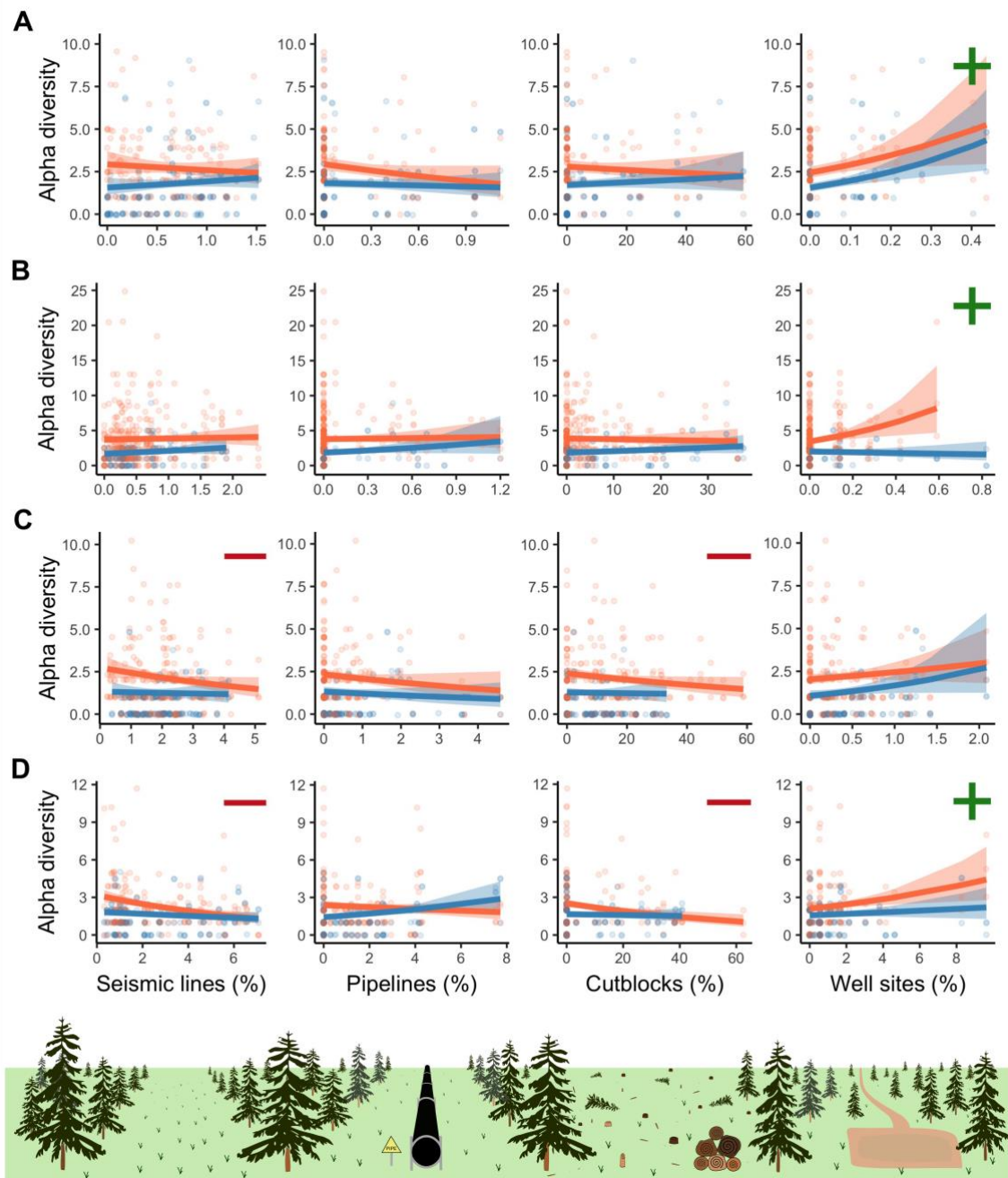
LS	Hypothesis	$k$	$\Delta$ AICc	AICc <sub>w</sub>	LL	RMSE
	<b>Productivity</b>	<b>7</b>	<b>0.00</b>	<b>1.00</b>	<b>-737.10</b>	<b>2.51</b>
LD-M	Natural heterogeneity	7	11.64	0.00	-742.92	2.66
	Null	5	18.93	0.00	-748.67	2.66
	Natural keystone structures	13	25.10	0.00	-743.17	2.69
	<b>Anthropogenic keystone structures</b>	<b>13</b>	<b>0.00</b>	<b>0.76</b>	<b>-608.47</b>	<b>1.56</b>
	Natural keystone structures	13	3.46	0.14	-610.20	1.59
HD-M1	Anthropogenic heterogeneity	7	4.37	0.09	-617.04	1.60
	Natural heterogeneity	7	9.70	0.01	-619.71	1.62
	Null	5	9.70	0.01	-621.79	1.63
	Productivity	7	12.37	0.00	-621.04	1.62
	<b>Anthropogenic heterogeneity</b>	<b>7</b>	<b>0.00</b>	<b>0.82</b>	<b>-1053.71</b>	<b>2.38</b>
	Anthropogenic keystone structures	13	3.23	0.16	-1049.07	2.38
HD-M2	Natural keystone structures	13	9.50	0.01	-1052.20	2.41
	Natural heterogeneity	7	10.20	0.00	-1058.81	2.40
	Null	5	10.82	0.00	-1061.18	2.39
	Productivity	7	14.38	0.00	-1060.90	2.39

Alpha diversity decreased with the proportion of seismic lines and cutblocks, but only in boreal landscapes (MD-B:  $\beta_{\text{Seismic}} = -0.13 \pm 0.13$ ,  $p = 0.043$ ;  $\beta_{\text{Cutblock}} = -0.14 \pm 0.14$ ,  $p = 0.494$ ; HD-B:  $\beta_{\text{Seismic}} = -0.30 \pm 0.15$ ,  $p < 0.001$ ;  $\beta_{\text{Cutblock}} = -0.14 \pm 0.08$ ,  $p < 0.001$ ). The relationship between alpha diversity and the proportion of seismic lines and cutblocks did not change between seasons in either boreal landscape (MD-B:  $\beta_{\text{Seismic:Seas}} = 0.10 \pm 0.25$ ,  $p = 0.435$ ;  $\beta_{\text{Cutblock:Seas}} = 0.10 \pm 0.32$ ,  $p = 0.532$ ; HD-B:  $\beta_{\text{Seismic:Seas}} = 0.19 \pm 0.20$ ,  $p = 0.062$ ;  $\beta_{\text{Cutblock:Seas}} = 0.12 \pm 0.11$ ,  $p = 0.062$ ). Alpha diversity was unaffected by the proportion of seismic lines and cutblocks in both mountain landscapes (HD-M1:  $\beta_{\text{Seismic}} = -0.07 \pm 0.17$ ,  $p = 0.454$ ; HD-M2:  $\beta_{\text{Seismic}} = 0.03 \pm 0.14$ ,  $p = 0.706$ ), and alpha diversity was unaffected by the proportion of pipelines in all landscapes (HD-M1:  $\beta_{\text{Pipeline}} = -0.28 \pm 0.30$ ,  $p = 0.066$ ; HD-M2:  $\beta_{\text{Pipeline}} = 0.03 \pm 0.22$ ,  $p = 0.782$ ; MD-B:  $\beta_{\text{Pipeline}} = -0.14 \pm 0.18$ ,  $p = 0.124$ ; HD-B:  $\beta_{\text{Pipeline}} = -0.06 \pm 0.10$ ,  $p = 0.238$ ).

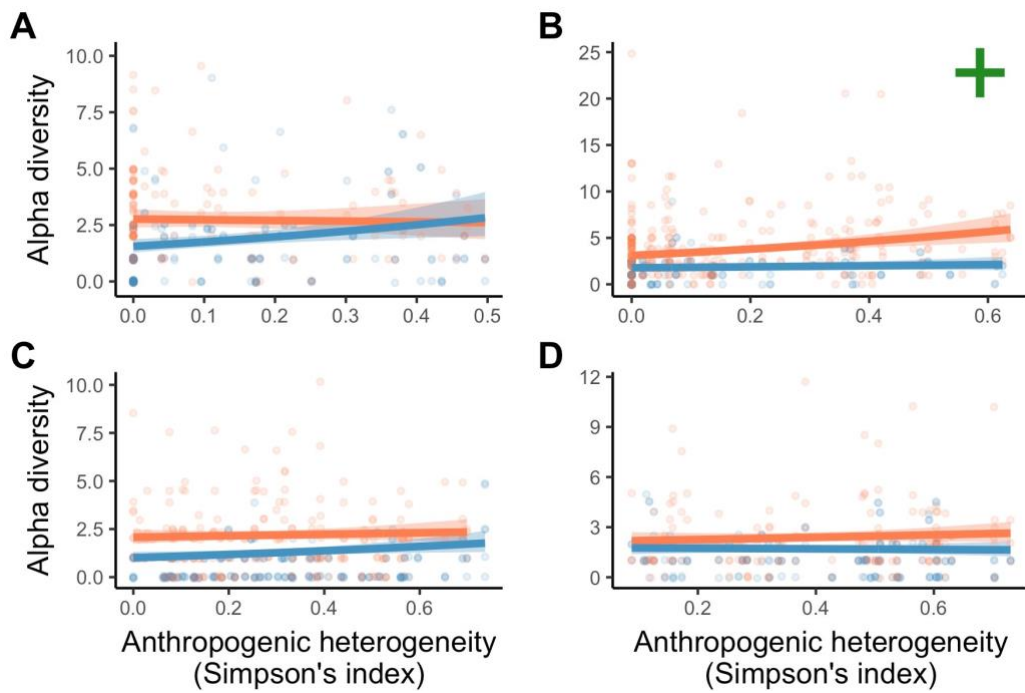
Alpha diversity only increased with anthropogenic heterogeneity in one of the highly industrialized mountain landscapes (HD-M1:  $\beta_{\text{Anthropogenic Heterogeneity}} = 0.18 \pm 0.09$ ,  $p < 0.001$ ; Figure 4). This relationship did not change between seasons ( $\beta_{\text{Anthropogenic Heterogeneity:Seas}} = -0.12 \pm 0.13$ ,  $p = 0.059$ ). Alpha diversity was unaffected by anthropogenic heterogeneity in the three other anthropogenically disturbed landscapes (HD-M1:  $\beta_{\text{Anthropogenic Heterogeneity}} = -0.02 \pm 0.13$ ,  $p = 0.779$ ; MD-B:  $\beta_{\text{Anthropogenic Heterogeneity}} = 0.04 \pm 0.11$ ,  $p = 0.517$ ; HD-B:  $\beta_{\text{Anthropogenic Heterogeneity}} = 0.06 \pm 0.12$ ,  $p = 0.324$ ).

**Table 2.3.** AICc tables of generalized linear mixed-effects models used to explain mammalian alpha diversity in boreal landscapes (LS) using different hypotheses. The covariates associated with each hypothesis are described in Table 2.1.  $k$  is the number of covariates; AICc<sub>w</sub> is the AICc weight; LL is the log-likelihood RMSE is the root mean-squared error using 10-fold cross-validation.

LS	Hypothesis	$k$	$\Delta$ AICc	AICc <sub>w</sub>	LL	RMSE
	<b>Productivity</b>	<b>7</b>	<b>0.00</b>	<b>0.67</b>	<b>-358.19</b>	<b>0.98</b>
LD-B	Null	5	1.91	0.26	-361.23	0.98
	Natural heterogeneity	7	5.92	0.03	-361.15	0.98
	Natural keystone structures	13	9.72	0.01	-356.63	0.98
	<b>Natural keystone structures</b>	<b>13</b>	<b>0.00</b>	<b>0.94</b>	<b>-632.90</b>	<b>1.32</b>
	Productivity	7	7.20	0.03	-642.80	1.33
MD-B	Natural heterogeneity	7	7.61	0.02	-643.00	1.33
	Anthropogenic heterogeneity	7	9.29	0.01	-643.85	1.33
	Null	5	10.00	0.01	-646.26	1.34
	Anthropogenic keystone structures	13	13.57	0.00	-639.68	1.33
	<b>Anthropogenic keystone structures</b>	<b>13</b>	<b>0.00</b>	<b>0.98</b>	<b>-540.10</b>	<b>1.50</b>
	Natural heterogeneity	7	8.59	0.01	-550.81	1.54
HD-B	Natural keystone structures	13	12.63	0.00	-546.42	1.53
	Productivity	7	16.25	0.00	-554.64	1.54
	Null	5	18.46	0.00	-557.82	1.54
	Anthropogenic heterogeneity	7	21.24	0.00	-557.13	1.54



**Figure 2.3.** Predicted relationships between mammalian alpha diversity and the proportional coverage of anthropogenic landscape figures in four variably industrialized northwest Nearctic landscapes: HD-M1 (A), HD-M2 (B), MD-B (C), and HD-B (D). Orange and blue curves show the predicted relationship during summer and winter, respectively. Orange and blue dots show raw alpha diversity during summer and winter, respectively. The direction of significant main effects of landscape features are shown with a positive or negative sign. Error bands around the predicted curves represent the 95% confidence interval.



**Figure 2.4.** Predicted relationships between mammalian alpha diversity and anthropogenic heterogeneity, calculated using Simpson's index, in four variably industrialized northwest Nearctic landscapes: HD-M1 (A), HD-M2 (B), MD-B (C), and HD-B (D). Orange and blue curves show the predicted relationship during summer and winter, respectively. Orange and blue dots show raw alpha diversity during summer and winter, respectively. The direction of significant main effects of landscape features are shown with a positive or negative sign. Error bands around the predicted curves represent the 95% confidence interval.

## Discussion

We found that the influence of anthropogenic landscape features on mammalian alpha diversity consistently outweighed that of natural features in highly industrialized landscapes, suggesting that anthropogenic determinants of alpha diversity now eclipse natural determinants in heavily modified environments. Conversely, we found no clear pattern in the relative influence of productivity, natural habitat heterogeneity, and natural keystone structures on mammalian alpha diversity across landscapes, suggesting that alpha diversity is shaped by different natural processes in different landscapes. We also found that alpha diversity increased with the coverage of petroleum-extraction well sites in each highly industrialized landscape, revealing that well sites are likely an anthropogenic keystone structure in highly anthropogenically disturbed landscapes. In contrast, we found that alpha diversity decreased with the proportion of seismic lines and forestry cutblocks, although only

in boreal landscapes.

Anthropogenic landscape features have long been known to alter species diversity, but they have not been previously shown to shape alpha diversity better than natural factors. This novel finding complements an earlier study showing the opposite pattern for mammal diversity at regional scales, where natural determinants of species diversity measured at 250 mi<sup>2</sup> well-outweighed anthropogenic determinants (Howard et al., 2019). Anthropogenic diversity determinants may be dominant at local but not regional scales because local diversity patterns reflect species' fine-scale movements and space use, which may abruptly and drastically change following anthropogenic disturbances (Fisher & Burton, 2018). For anthropogenic disturbances to shift regional diversity to a similar degree, they must induce species' extirpations or invasions, requiring more time and often more intensive anthropogenic pressures (Howard et al., 2019). Additionally, local diversity is often less strongly explained by the environment than regional diversity (Field et al., 2009), implying that anthropogenic diversity determinants do not to be as strong to outweigh natural determinants at local scales as they do at regional scales.

The keystone structures hypothesis has previously focused on natural keystone structures (Tews et al., 2004), but we extend the concept to anthropogenic keystone structures in showing that petroleum-extraction well sites increase alpha diversity—interpreted as aggregating multiple species—in heavily industrialized landscapes. Well sites likely increase mammalian alpha diversity by their relatively small area and proximity to forest cover, providing early seral vegetation on which herbivores can forage with relatively low perceived risk (Lendrum et al., 2018). These conditions likely attract herbivorous species, like meadows and other natural forest clearings (Balčiauskas et al., 2017), that subsequently attract predator and scavenger species (Keim et al., 2011). Despite requirements for well site operators to restore decommissioned sites, early seral vegetation on well sites often remains in an arrested successional state for decades (Lupardus et al., 2019), and with their ubiquity across the industrialized northwest Nearctic, well sites likely have long-lived and widespread impacts on mammalian alpha diversity.

Linear corridors and large polygonal forest clearings (Fisher & Wilkinson, 2005) fragment natural habitats and alter species' movements, often repelling top predators (Crooks et al., 2017). While this pattern aligns with our finding that seismic lines and cutblocks decreased alpha diversity in boreal landscapes, top predators in the northwest Nearctic commonly travel along seismic lines (Dickie et al., 2020; Tattersall et al., 2020). Seismic lines may therefore decrease alpha diversity because they are used by top predators that

subsequently repel subordinate predator and prey species (Berger-Tal & Saltz, 2019), in which case species interactions may be a key proximate determinant of alpha diversity. It is interesting, however, that seismic lines did not decrease alpha diversity in mountain landscapes. This is potentially because seismic lines are not dense enough in mountain landscapes to alter alpha diversity.

My findings cast doubt on the existence of universally dominant natural determinants of alpha diversity, as productivity, landscape heterogeneity, and potential keystone structures variably influenced alpha diversity between landscapes. In fact, the inability for any landscape characteristic to explain alpha diversity better than the null model in the lowly anthropogenically disturbed (but recently burned) boreal landscape supports the proposition that fine-scale diversity is driven largely by stochastic processes (O'Brien, 2006). However, it is necessary to emphasize that we considered only a limited set of possible diversity determinants (Atauri & De Lucio, 2001), and that we measured alpha diversity over 30 days, centering our conclusions on species' short-term space use. Additionally, we only considered local landscape characteristics (within 2.5 km of each camera), negating potential influence from landscape characteristics at larger spatial scales (e.g., the proportion of cutblocks within 5 km of each camera). In turn, future studies may consider additional environmental characteristics and measure alpha diversity over different time frames in attempt to reconcile apparent landscape-level differences in how species diversity is determined. Nonetheless, our analysis will help inform future studies that aim to compare trap data from multiple landscapes, supporting a valuable type of analysis for which there is currently little empirical guidance (Steenweg et al., 2017).

Overall, our findings suggest that anthropogenic activities catalyze major shifts in how alpha diversity is determined and distributed. With evidence that landscape restoration can re-establish mammal community dynamics (Beirne et al., 2021), it is possible that landscape restoration can mitigate the influence of anthropogenic diversity determinants. Without restoration, however, anthropogenic diversity determinants will likely persist, if not strengthen, from continued anthropogenic activities.

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## ESTIMATING DENSITY FOR MAMMALS UNDER VARYING ECOLOGICAL CONDITIONS

### **Preface for Oil Sands Monitoring**

The Oil Sands Monitoring Program has been seeking to use density estimates of mammals as a metric of change in the region<sup>30</sup>. Density is an ‘essential biodiversity variable’<sup>31</sup> and is needed to understand how the numbers of animals change over time – especially species of cultural importance such as moose, and species of conservation concern such as caribou. Aerial Ungulate Surveys are conducted by Alberta Government<sup>32</sup>, and carry their own values, opportunities, errors, and risks. Caribou density is rigorously estimated through fecal surveys paired with DNA analysis and spatial explicit capture-recapture analysis<sup>33</sup>. However it is important to estimate density of multiple mammal species simultaneously<sup>9</sup>, especially to inform Investigation of Cause. Camera trapping<sup>34</sup> can provide data on species detections across space, but as most northern species lack individual marks traditional capture-recapture or mark-resight models cannot be used, so we rely on unmarked models<sup>10,35</sup>. The performance of these models is highly variable<sup>1,36-41</sup>: last year we assessed two forms of unmarked models, the TIFC model developed by ABMI<sup>42</sup> and the increasingly widely-used spatial count (SC) models of Chandler and Royle<sup>43</sup>. We showed marked differences among the model constructs, with TIFC varying widely among landscapes, and years<sup>44</sup>, and SC models. Such variability highlights that more work is needed to understand the models, and that the conclusions drawn from them should be further tested. However, as we lack any “true” measure of mammals’ abundance in the wild, we are always left wondering how close we are.

We skirted this problem using an “experimental” test of SC models as a mode of monitoring for OSM mammals. We tested SC density models on a wolf population subject to lethal predator control. The wolf cull implemented at Christina Lake is a rare and useful opportunity to test these models, as we have three years of pre-control and 1 year of post-control data. If SC models are recovering biological correct population estimates, then we should see three years of population stability followed by a decline.

SC models were successful in recovering the decline in wolf densities following lethal predator control. This trend was successfully observed, even though SC models are known to be rigid in their density estimates from year to year; a comparison with TIFC models produced wide variations annually in TIFC model estimates that were not observed in SC models, and there was some concern that the problem was with SC models’ conservatism<sup>44</sup>.

We show this is not the case and suggest SC models are much less to pick up a false signal of density changes annually. This lends much confidence in their use for future OSM trend monitoring and investigation of cause.

### **Why is the development of methods and indicators important for OSM in an EEM framework?**

Indicators, as references in the TBM conceptual model, are components of the environment: in the case of mammals, species of ecological and social importance, such as moose. However, “moose” is not a measurable indicator; some measure of moose is the indicator. Potential metrics include individual space-use, population distribution, relative abundance, community diversity, and population density. These metrics do not necessarily scale together, because they derive from different ecological processes<sup>29,45-47</sup>. In effect, each one tells a unique story about the effect of OS development on mammals, each one worth knowing if you want to understand cause-and-effect relationships. Moreover, these metrics have different sensitivities; a change in one metric may not be picked up as a change in another, even when that indicator is changing too.

Density is the hardest metric to derive, because it is the “closest” to biological reality of this lot. It may be the most sensitive of the lot as well. Finally, it is also one of the most useful for harvested game species, as AEP sets its harvest quotas based on estimated population densities. The drive for density is a global pursuit, and to maintain global relevance OSM needs to adopt density metrics that are recognized as robust and sensitive – particularly if they are to be used *and defended* in adaptive decisions in an EEM framework. Understanding how a density metric performs in an experimental situation therefore gives the TBM TAC ammunition for decision-making around indicators, thresholds, and triggers.

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**Authors:** Andrew Ladle<sup>1\*</sup>, Andrew F. Barnas<sup>1\*</sup>, Joanna M. Burgar<sup>1,2</sup>, Catherine C. Sun<sup>2</sup>, A. Cole Burton<sup>2</sup>, Brad Anholt<sup>3</sup>, Jason T. Fisher<sup>1</sup>.

<sup>1</sup> School of Environmental Studies, University of Victoria, Victoria, V8W 2Y2, British Columbia, Canada

<sup>2</sup> Department of Forest Resources Management, University of British Columbia, 2424 Main Mall, Vancouver, V6T 1Z4, Canada

<sup>3</sup> Biology Department, University of Victoria, Victoria, V8W 2Y2, British Columbia, Canada

\*Equal first authors

## Introduction

Lethal predator control (LPC) as a means of reducing hunting pressure on game species is attributed to the arrival of European colonists in the 16th century<sup>48</sup>. Since its inception, LPC has been implemented to achieve several goals including livestock protection<sup>49</sup>, invasive predator control<sup>50</sup>, or conservation of prey species<sup>51,52</sup>. While these practices have been ongoing for hundreds of years, the reliability of LPC has recently been subject to critical examination, as many LPC programs take place without evaluating whether programs were “successful” in achieving their goals: a “shot in the dark”. (Treves et al. 2016, *citations within*). Analysis of predator demographic changes is often ad hoc, with ‘results’ merely a tally of predators killed<sup>53</sup>. Further, the 20th century witnessed a societal shift from predator eradication towards increased tolerance, conservation, and even reintroduction of predators<sup>54</sup>. This shift, coupled with evidence questioning the efficacy of predator control measures relative to non-lethal approaches<sup>53,55</sup>, is likely to further erode public support for LPC<sup>52,56</sup>. LPC is likewise controversial among scientists, compelling some to call for censoring predator-control research on ethical grounds, even when the goal is to prevent extirpation of threatened and endangered prey species<sup>57</sup>. As conservation policies are often a trade-off between public opinion and scientific evidence, critical scientific evaluations of LPC program are necessary to improve our understanding of their impacts and facilitate evaluation of their capacity as a conservation tool – but rarely (if ever) accomplished.

As well as a basic accounting of population size pre- and post- LPC, another often overlooked aspect is the broader ecological impacts and unintended consequences of predator removal<sup>58</sup>.

Removal of large predators can lead to drastic restructuring of food webs due to their role as apex consumers<sup>59</sup>, which may eventually have downstream negative impacts on livestock or species of conservation concern. For example, removal of large predators can provide open niches whereby

smaller predators invade and kill livestock<sup>60</sup>. Counter-intuitively, removal of predators can also lead to compensatory reproduction, ultimately increasing predator population growth rate and densities in following years<sup>61</sup>. As LPC programs are often financially (and ecologically) costly, understanding and minimizing unintended consequences warrants further investigation.

Unfortunately, evaluating such programs requires reliable data on predator occurrence to estimate population densities, which is often a difficult and imprecise endeavour. There has been extensive interest in developing reliable, long-term, financially feasible methods of estimating predator density, particularly for large, cryptic, wide-ranging mammalian predators. Occupied aircraft surveys are notoriously imprecise, prohibitively expensive<sup>62</sup>, and are a leading cause of work-related mortality for wildlife biologists<sup>63</sup>. Satellite-based surveys are promising for large mammal surveys but are typically used in regions with little cloud cover and open landscapes<sup>64</sup>. Similarly, drone-based surveys are rapidly becoming integrated in wildlife sciences<sup>65</sup>, although they are not yet being used for landscape-scale surveys required for large terrestrial mammals with large home ranges (but see Patterson et al. 2015). The most promising methods to evaluate LPC programs are camera traps (CTs; Burton et al. 2015) as their cost-effectiveness and ability to capture replicable data on multiple species offer a potential solution for species monitoring globally<sup>9,25</sup>. Using CT data to inform spatially-explicit density estimation is now familiar for marked species<sup>67,68</sup>, and newer Spatial Count (SC) models for fully unmarked species have been proposed<sup>69,70</sup> albeit with limited application and evaluation (but see Burgar et al. 2019). One of the primary benefits of CTs for evaluating LPC programs is the ability to capture data on focal predator abundance, but with the additional benefit of simultaneously monitoring other species (see Fisher, et al.<sup>71</sup>). These benefits, along with the integrated spatial data that comes with CTs means these tools have huge potential for evaluating LPC programs.

Here we illustrate an example of evaluating effectiveness and unintended consequences of lethal predator removal by examining management actions intended to preserve declining boreal woodland caribou (*Rangifer tarandus*) in eastern Alberta, Canada. Boreal woodland caribou are in severe decline (Hervieux et al., 2014), driven primarily by a complex interaction between wolves (*Canis lupus*) and industrial linear feature footprints. Range-expanding white-tailed deer (*Odocoileus*

*virginianus*) inflate wolf population size, while linear features increased movement by wolves, both resulting in increased encounter rates with caribou <sup>72,73</sup>. As part of efforts to reverse this decline and release woodland caribou from predation pressures, provincial governments have initiated targeted wolf control via lethal removal <sup>51</sup>. We use data collected from a CT array and recently developed SC models <sup>69,70</sup> to demonstrate wolf removal results in a marked reduction in estimated wolf abundance and density, but also that wolf removal resulted in altered wolf activity distribution and home range size. We discuss the broader ecological implications of wolf removal, the potential effectiveness of this practice for caribou conservation, and the potential applications of CT methods in future evaluations of LPC methods.

## **Methods**

### *Study area*

Our study area is an approximately 3,000 km<sup>2</sup> area (Fig 1A) within the East Side Athabasca River woodland caribou herd home range and is dominated by spruce (*Picea spp.*) and aspen (*Populus tremuloides*) forest. These sites host a variety of wildlife including wolf, caribou, white-tailed deer, moose (*Alces alces*), and black bear (*Ursus americanus*). The region contains a high-density footprint of linear features comprised of pipelines, powerlines, and seismic exploration, as well as other industrial features (i.e., oil well sites). For a more in-depth description of the area, see <sup>6</sup>.

### *Camera trap monitoring*

We detected wolves using remotely triggered trail cameras (Reconyx PC900 Hyperfire, Holmen, WI, USA) at n = 62 (pre-control, Fig 1B) and 55 (post-control, Fig 1C) sites (Table 1) selected using a stratified random sampling design. Cameras collected a series of 3 photos when wildlife triggered the infrared sensor (for additional information and technical details see Supporting Information: Camera Sampling Design, Burgar et al. 2019). Cameras were active on the landscape for an average of 340 days pre- and 341 days post-control, for a total of 21,084 and 18,752 trap days for each monitoring period (Table 1). Images were reviewed in Timelapse ImageAnalyzer 2.0 <sup>20</sup> for wolf presence, and events were classified as independent when wolf detections were separated by more than 30 minutes.

### *Density estimation using camera detections*

We used SC models to estimate the abundance of wolves pre- and post- wolf control. SC models extend beyond traditional spatial capture-recapture (SCR) models, using spatial correlation of observed counts of unmarked individuals at camera detector locations to estimate the number and spatial distribution of latent individual activity centers. The observed counts  $n_j$  at a site  $j = 1, 2, \dots, J$  on any occasion  $k = 1, 2, \dots, K$  are the sum of individual encounters, which are unobserved (i.e., latent) because individuals  $i = 1, 2, \dots, N$  in the population  $N$  cannot be distinguished. The SC model is still built according to these latent individuals and their detections, with detection rate decreasing from a baseline  $\lambda_0$  as a function of distance (e.g. standard half-normal function) and scale parameter  $\sigma$  that also determines the degree of spatial correlation between counts among sites<sup>69,70</sup>. This individual-level formulation enables a parameter-expanded data augmentation approach to estimate  $N$ <sup>74,75</sup>, whereby an imaginary super-population of size  $M > N$  is specified and each individual  $z_i = 1, 2, \dots, M$  is a member of  $N$  with probability  $\psi$ . The locations  $s_i = 1, 2, \dots, N$  of individuals are modeled as a spatial point process over a state-space  $S$  that is large enough to ensure non-zero detection probability of individuals at the edge of the CT sampling array.

Analysis was undertaken within a Bayesian framework, using vague uniform prior distributions for  $\lambda_0$  (between 0 and 1) and  $s_i$  (within the state space, see below), while  $\sigma$  was informed by wolf home range sizes in the region obtained using location data from radio collared individual wolves (mean home range size = 1121.67 km<sup>2</sup>, range = 664 – 1480 km<sup>2</sup>; Burgar et al., 2019 – Supporting Information: Model Specification), using a gamma distribution (shape = 120, scale = 150; Chandler & Royle, 2013). We set  $M = 500$  and the state space  $S = 7366$  km<sup>2</sup> pre-control (Fig 1B) and  $S = 7266$  km<sup>2</sup> post-control (Fig 1C), which translated as a 20 km buffer around each period's camera array. As we had multiple years of data pre-control, we used a multi-session approach, whereby we obtained individual estimates of  $N$  for each annual period, by using shared prior information for  $\lambda_0$  and  $\sigma$  across sessions, while  $s_i$ ,  $z_i$ , and therefore  $N$  were allowed to vary by session. A single-session model was run for the post- control model.

We initialized 3 chains with 10,000 burn-in Markov chain Monte Carlo (MCMC) iterations, following by sampling over 100,000 iterations. Chains were assessed for convergence using the Gelman-Rubin statistic  $R_c$  and were accepted as adequate if  $R_c < 1.1$ <sup>70</sup>. We report median posterior

estimates of density with 95% Bayesian Credible Intervals (BCI). Posterior estimates of activity center coordinates,  $s_i$ , were used to produce spatial maps of wolf density across  $S$ .

## Results

The number of wolf detections per 100 days was considerably lower post-control (0.22 detections per 100 days) relative to pre-control (mean = 0.80 detections per 100 days; Table 1). Similarly, the proportion of sites where at least one wolf was detected was lower post-control (0.38) compared to pre-control (mean = 0.74). We recorded 0-34 independent detections of wolves on cameras prior to wolf control, but only 0-8 independent detections post wolf control.

### *Density Estimation*

We estimated a median  $N = 42$  (Fig 2, BCI = 25 – 72) wolves for the pre-control monitored period (2011-2012 = 45, BCI = 28 – 77; 2012-2013 = 40, BCI = 23 - 70; 2013-2014 = 42, BCI = 25 – 72; Table S1), for a density estimate of 0.42 wolf activity centers per 100 km<sup>2</sup> (Fig 2). We estimated a median  $N = 9$  (Fig 2, BCI = 4 - 33) post-control (Table S1), which translated to a density of 0.12 wolf activity centers per 100 km<sup>2</sup> (Fig 2). Estimates of  $\sigma$  post-wolf control were larger (median = 0.79, BCI = 0.66 – 0.94) compared to pre-wolf control (median = 0.46, BCI = 0.37 – 0.59) (Fig 2). Due to  $\sigma$ 's relationship with home range size<sup>69</sup>, this result implies that the average wolf home-range size was larger post-control. But importantly, in these models a decrease in  $\lambda_0$  necessitates an increase in  $\sigma$ , therefore this result should be interpreted with caution. For further details on model estimates and diagnostics see Supplemental Materials: Model Results.

### *Activity center distributions*

Spatial variation in wolf activity center density varied across our state space, ranging up to 3 activity centers per 100 km<sup>2</sup> prior to wolf control, and only up to 1 activity center per 100 km<sup>2</sup> after lethal control. Post-control, wolf activity centers were diminished within a high-density area in the north-west of the study area, but wolves persisted in the north-east region, albeit at a lower density compared to pre-control years.

## Discussion

Unsurprisingly, LPC of wolves resulted in a lower estimated wolf abundance and density in the post-control period, but reductions were accompanied by increased size of wolf

activity centers and altered spatial distributions. Abundance estimates are a widely used metric in conservation policy planning <sup>76</sup>, but our findings highlight an important critique of many LPC programs in that there can be unintended ecological consequences of predator removal <sup>53</sup>. These findings would have been very difficult to observe with alternative data collection methods, which demonstrates the important contribution of CTs to informing conservation actions.

Given that wolves are a leading cause of mortality for caribou in western Alberta <sup>51</sup>, the lower estimated abundance of wolves in the post-cull period should logically result in reduced predation of caribou. Several studies have shown promising results of wolf removal increasing caribou population growth (Hervieux et al. 2014; Serrouya et al. 2019, but see Harding et al. 2020). However, these results may be short lived <sup>78</sup>, as wolf populations can experience large mortality rates, then recover due to high reproductive output <sup>79</sup>. Our unexpected findings have implications for the effectiveness of wolf culling on caribou conservation, as increased wolf home ranges may reflect expansion of remaining individuals into neighbouring territories, potentially due to reduced scent marking cues from neighbouring packs <sup>80</sup>. How increased home range and altered spatial distributions impact other members of the ecosystem remains unseen, which highlights the need for multispecies monitoring to fully understand impacts of LPC programs. Although we did not investigate the effects of wolf removal on caribou populations, our approach captured ecological phenomenon beyond wolf abundance estimates following removal, and highlights a method which can be used to investigate multiple interacting species <sup>6,9</sup>.

We emphasize that SC estimates come with a high degree of uncertainty: our estimated BCIs were large, an issue previously highlighted regarding SC models <sup>9,69</sup>. However, informed prior distributions based on home-range information from radiocollared individuals likely improved precision. A key caveat of our analyses here are that density estimates reflect the density of “activity centers” rather than true wolf population density,

partly due to uncertainty of wolf pack size from CT data. Quantifying a “group size” estimate using the number of individual wolves photographed per independent camera event can help modify the estimate, reflecting individual density as opposed to pack density, however more explicit statistical methods are required for such an analysis. There are other promising methods to be explored using CT data such as Spatial Mark-Resight (SMR) models <sup>81</sup> – whereby a small subset of the population is individually identifiable through tagging or radiocollaring, which improves density estimates but at a cost both financially and in terms of increased invasiveness. Spatial Partial Identity Models (SPIM) where sex, pelage, or other classes separates a population into categories, allow for partial identification and therefore informs the number of unique individuals, likewise improving estimates <sup>82</sup>. These models show potential with certain species, specifically ungulates that have highly visible characteristics such as presence of antlers and number of antler points. Regarding wolves, coat color in populations where this is a highly variable trait might offer increased precision in estimates, as well as including marked individuals such as radiocollared animals, when identification of the exact individual is unclear. However, since the goal to understand the effectiveness of predator control is recovery of caribou numbers, SPIM could be an excellent step forward in validated the success of this objective.

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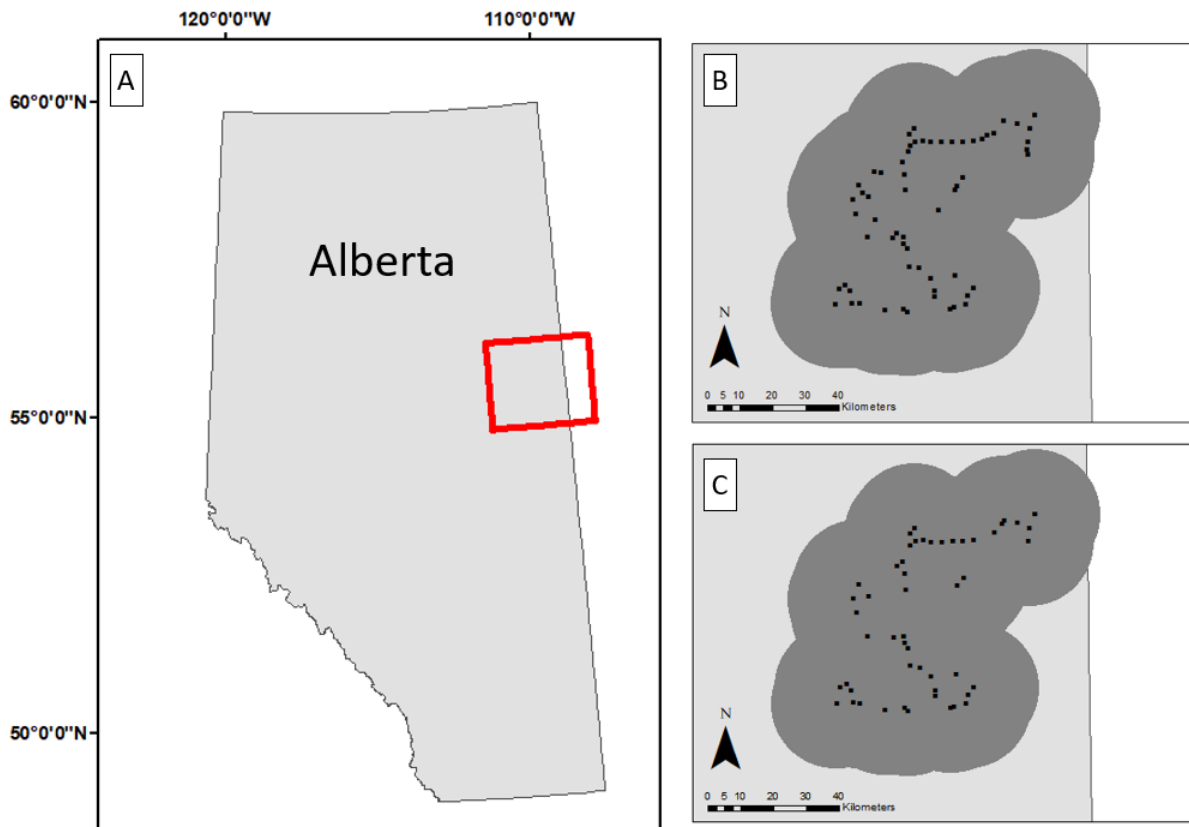
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1 **Table 1. Detections of wolves (*Canis lupus*) in eastern Alberta by remote camera traps during**  
 2 **periods prior to wolf control (2011 – 2014, n = 62 cameras) and post wolf control measures**  
 3 **(2017, n = 55 cameras).**

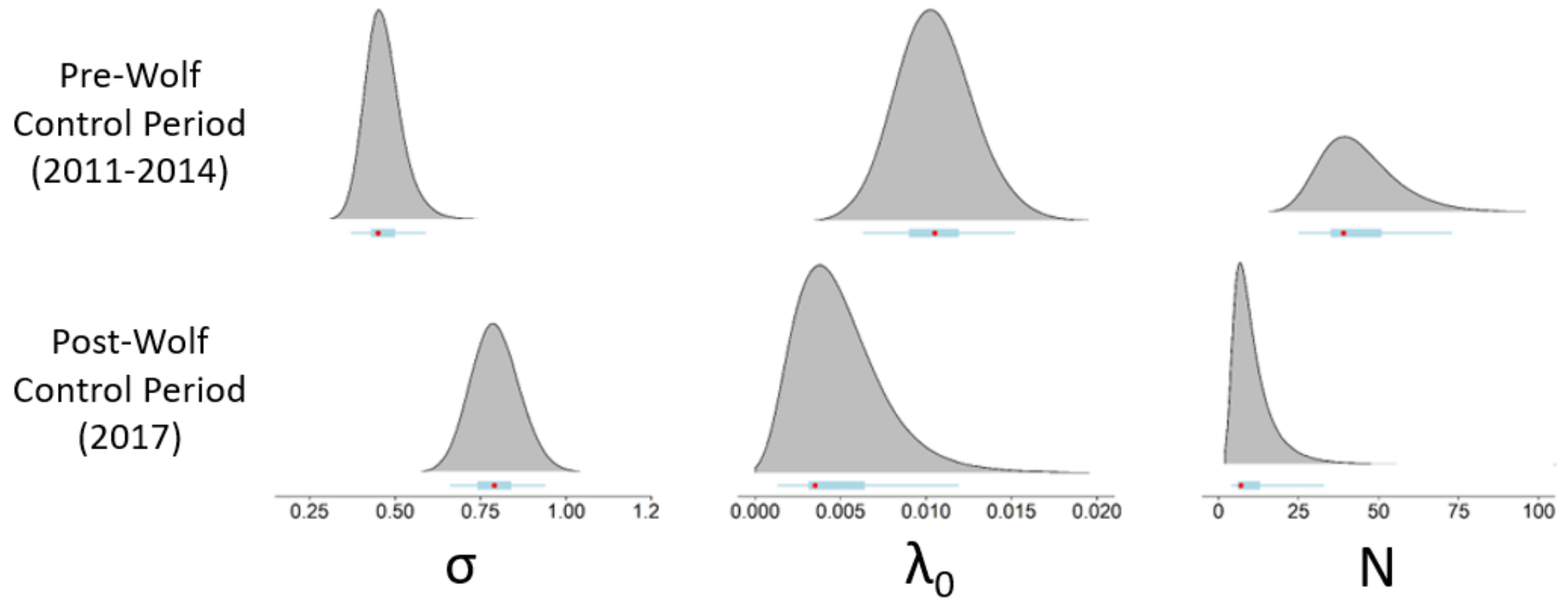
PERIOD	YEAR	TOTAL DETECTIONS*	DETECTIONS PER 100 TRAP DAYS	PROPORTION OF SITES DETECTED
PRE- CONTROL	2011-2012	189	0.89	0.79
	2012-2013	156	0.71	0.71
	2013-2014	161	0.80	0.71
POST- CONTROL	2017	42	0.22	0.38

4 \*Where detections are considered independent if separated by 30 mins  
 5



6  
 7 Figure 1. Map of the study area. A) Alberta, Canada, with extent indicator of study location.  
 8 B) Pre-wolf control camera locations (n = 62) along with 20km state-space buffer used for  
 9 modelling approach. C) Post-wolf control camera locations (n = 55) with similar 20km  
 10 buffer.  
 11

12



13

14 Figure 2. Posterior probability distributions for the multi-session pre-control years model (2011-2014) and post-control model (2017), for  $\sigma$ ,  $\lambda_0$ ,

15 and  $N$ . Red dot represents the median, with the inter-quartile (50%) and BCI (95%) in blue.

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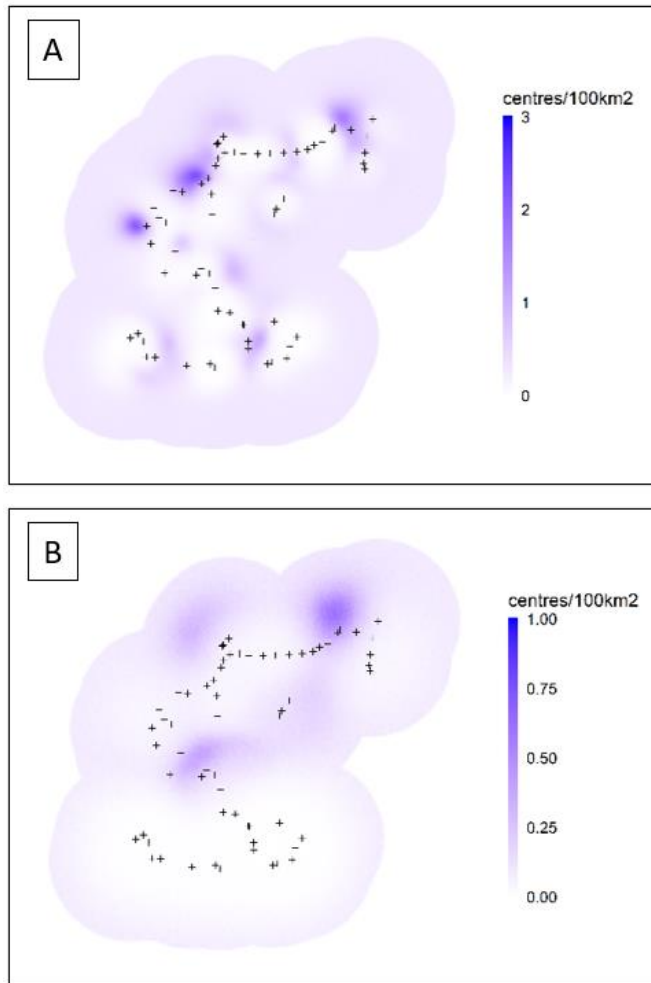


Figure 3. Estimated activity centre density distribution from A) pre-wolf control years (2011-2014) and, B) post-wolf control year (2017). Black crosses represent camera locations.

## **Supplementary Information**

### **Camera Sampling Design**

To estimate wolf (*Canis lupus*) density pre- and post-control methods, we used an array of remote camera traps. Between October 2011-2014 (pre-control) and October 2017-2018 (post-control), we placed a single Reconyx PC900 Hyperfire™ infra-red remote camera (Holmen, WI, USA) at designated sites. Sites were selected using a stratified random design based on strata varying by canopy cover, tree species and topography (Fisher & Burton, 2018). Cells were selected based on the strata from a 1 x 1 km grid, and un-baited cameras were placed on game trails to maximise detectability and conforming to at least 2km distance between adjacent sites.

Cameras were checked annually in the summer to perform maintenance and collect data. Cameras were placed approximately 0.5m off the ground, affixed to trees using cable locks. We applied scented lure to nearby trees to increase detections of nearby wildlife. Cameras were programmed with a “timelapse” function, set to record a single picture each day at noon to ensure the camera was still operational on each day.

Once data was collected, images were reviewed for wolf presence by trained technicians using *Timelapse* software. We did not consider group sizes when multiple wolves were detected on camera at once, rather we treated independent detections as presence/absence in our given time window.

## Model Results

Table S1. Posterior parameter estimates for N, sigma and lam0 for all monitored years (complete dataset with informed sigma prior). Summary statistics include mode, mean, median and 95% and 50% Bayesian credible interval ranges.

Parameter	Year	mode	mean	0.025	0.25	median	0.75	0.975
N	2011-2012	43	47	28	38	45	54	77
	2012-2013	38	42	23	33	40	48	70
	2013-2014	39	43	25	35	42	50	72
	2017-2018	7	11	4	6	9	13	33
D	2011-2012	0.49	0.47	0.28	0.38	0.45	0.53	0.76
	2012-2013	0.49	0.42	0.23	0.33	0.40	0.48	0.69
	2013-2014	0.49	0.43	0.25	0.35	0.42	0.49	0.71
	2017-2018							
sigma	2011-2014	0.45	0.47	0.37	0.43	0.46	0.50	0.59
	2017-2018	0.79	0.79	0.66	0.74	0.79	0.84	0.94
lam0	2011-2014	0.011	0.011	0.0063	0.0090	0.010	0.012	0.015
	2017-2018	0.0035	0.005	0.0013	0.0031	0.0045	0.0064	0.012

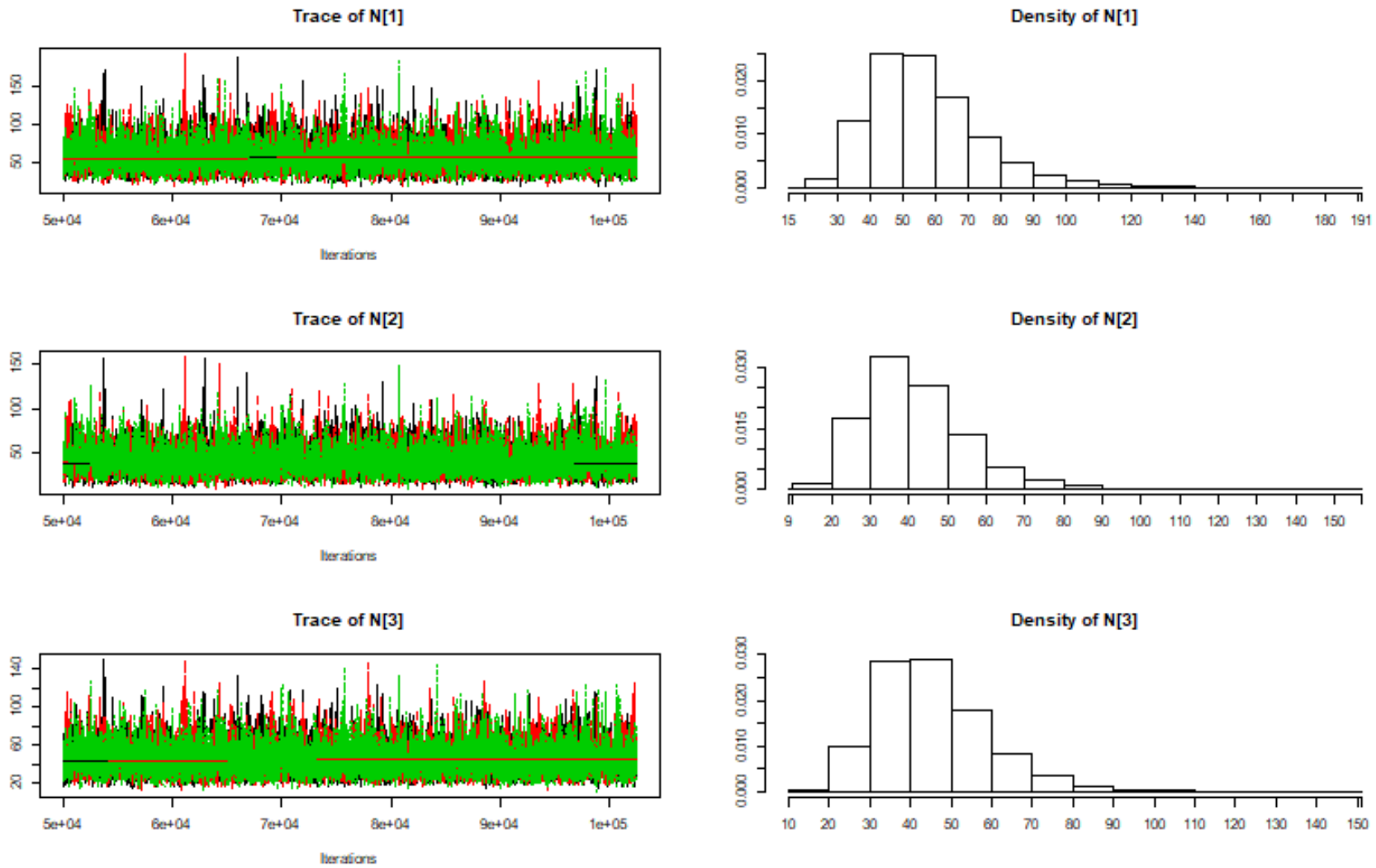


Fig S1a. Traceplots for posterior estimates of pre-control abundance for years 2011-2012 (N[1]), 2012-2013 (N[2]) and 2013-2014 (N[3]).

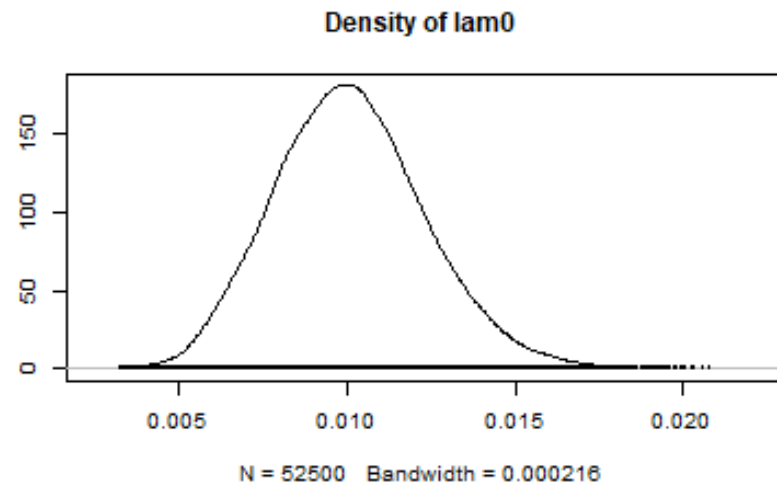
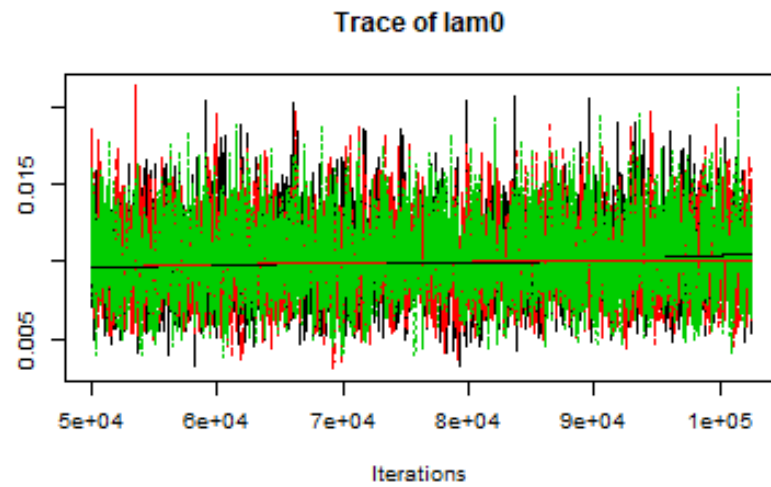
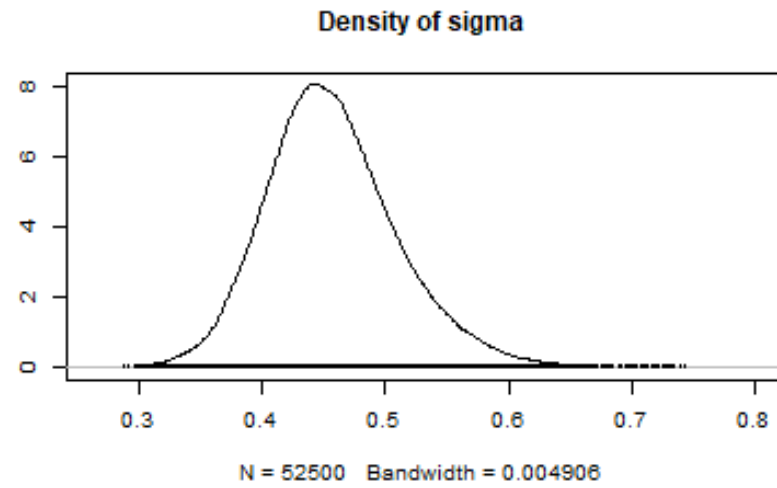
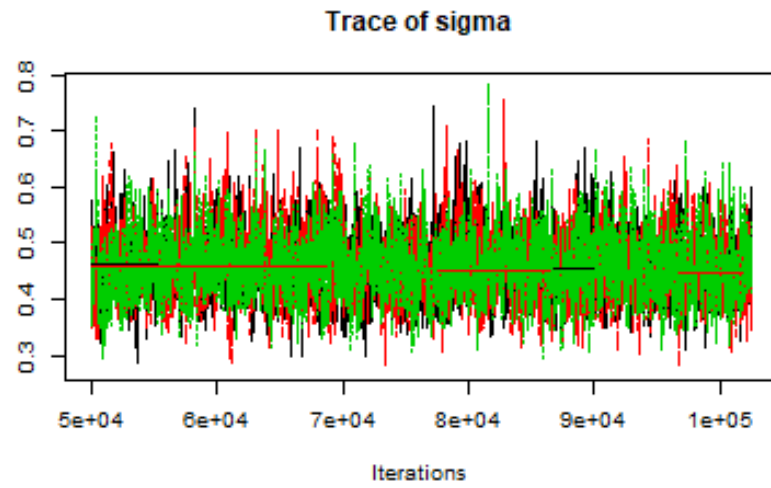


Fig S1b. Traceplots for posterior estimates of  $\sigma$  and  $\text{lam0}$  for the multi-season, pre-control model.

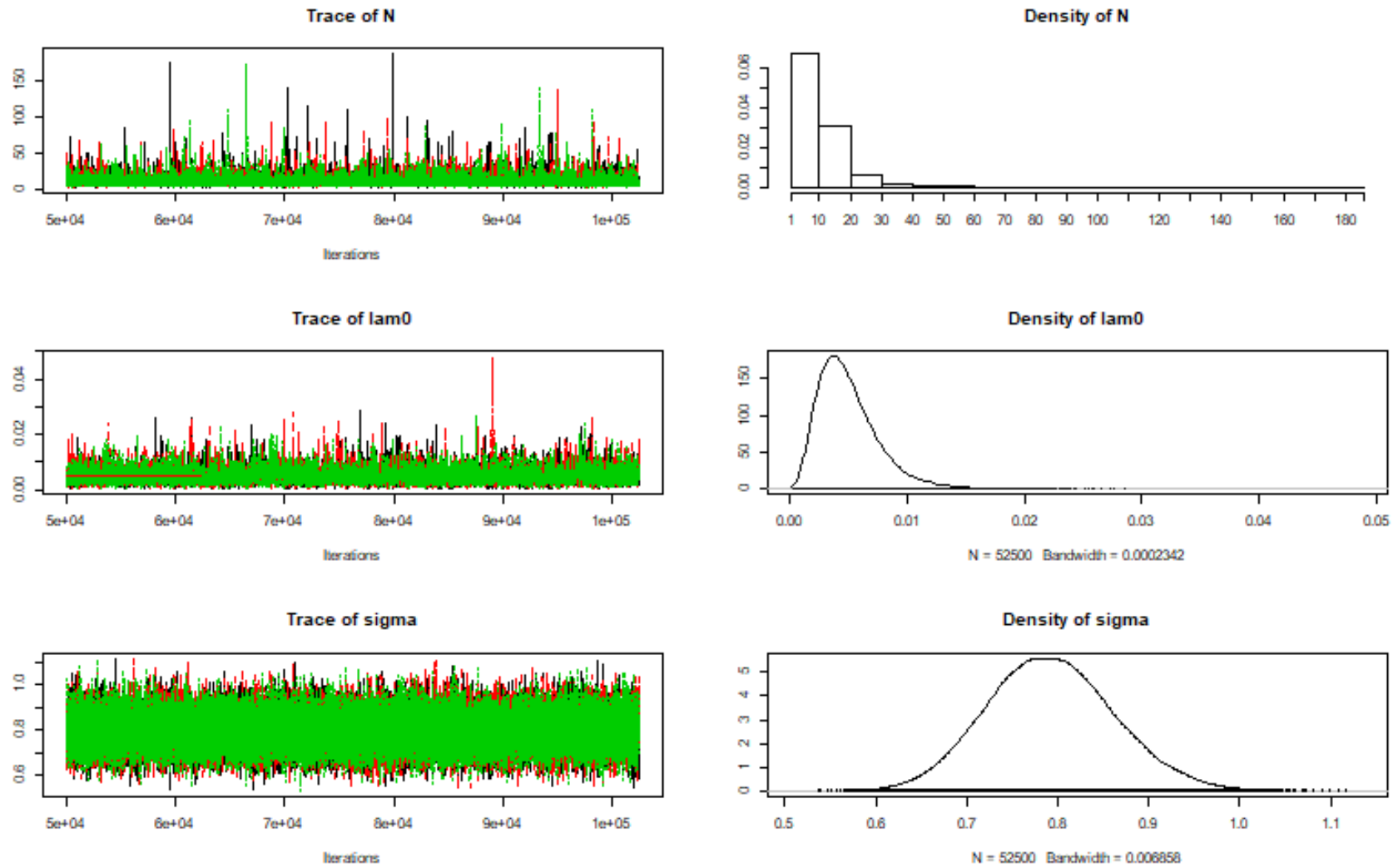


Fig S2. Traceplots of posterior estimates for the post-control (2017-2018) model for abundance,  $lam0$ , and  $sigma$ .

## Posterior predictive checks

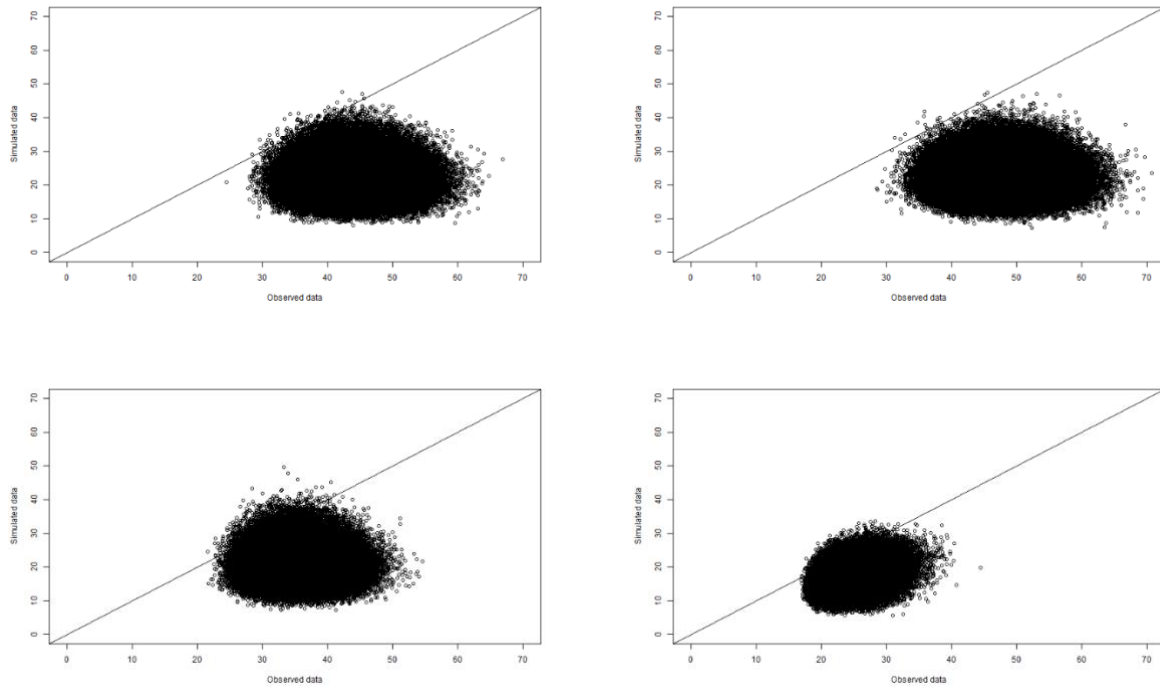


Fig S3. Goodness of fit plots for pre (a,b and c) and post (d) predator control spatial count models. ‘Observed’ is the summed errors of the observed – expected, and ‘Simulated’ is the summer errors of the simulated – expected.

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