



# How landscape traits affect boreal mammal responses to anthropogenic disturbance

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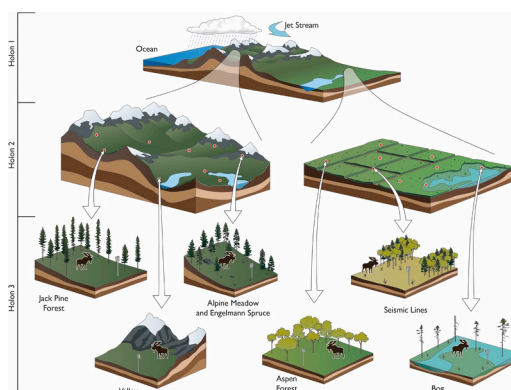
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## HIGHLIGHTS

- Ecological processes change across spatial scales and landscape contexts.
- Camera traps deployed across multiple landscapes help investigate mammal responses.
- Mammal response to local disturbance depends on landscape level disturbance context.
- Generalized trends across study areas help support broad conservation actions.

## GRAPHICAL ABSTRACT



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## ABSTRACT

Understanding mammalian responses to anthropogenic disturbance is challenging, as ecological processes and the patterns arising therefrom notoriously change across spatial and temporal scales, and among different landscape contexts. Responses to local scale disturbances are likely influenced by landscape context (e.g., overall landscape-level disturbance, landscape-level productivity). Hierarchical approaches considering small-scale sampling sites as nested holons within larger-scale landscapes, which constrain processes in lower-level holons, can potentially explain differences in ecological processes between multiple locations. We tested hypotheses about mammal responses to disturbance and interactions among holons using collected images from 957 camera

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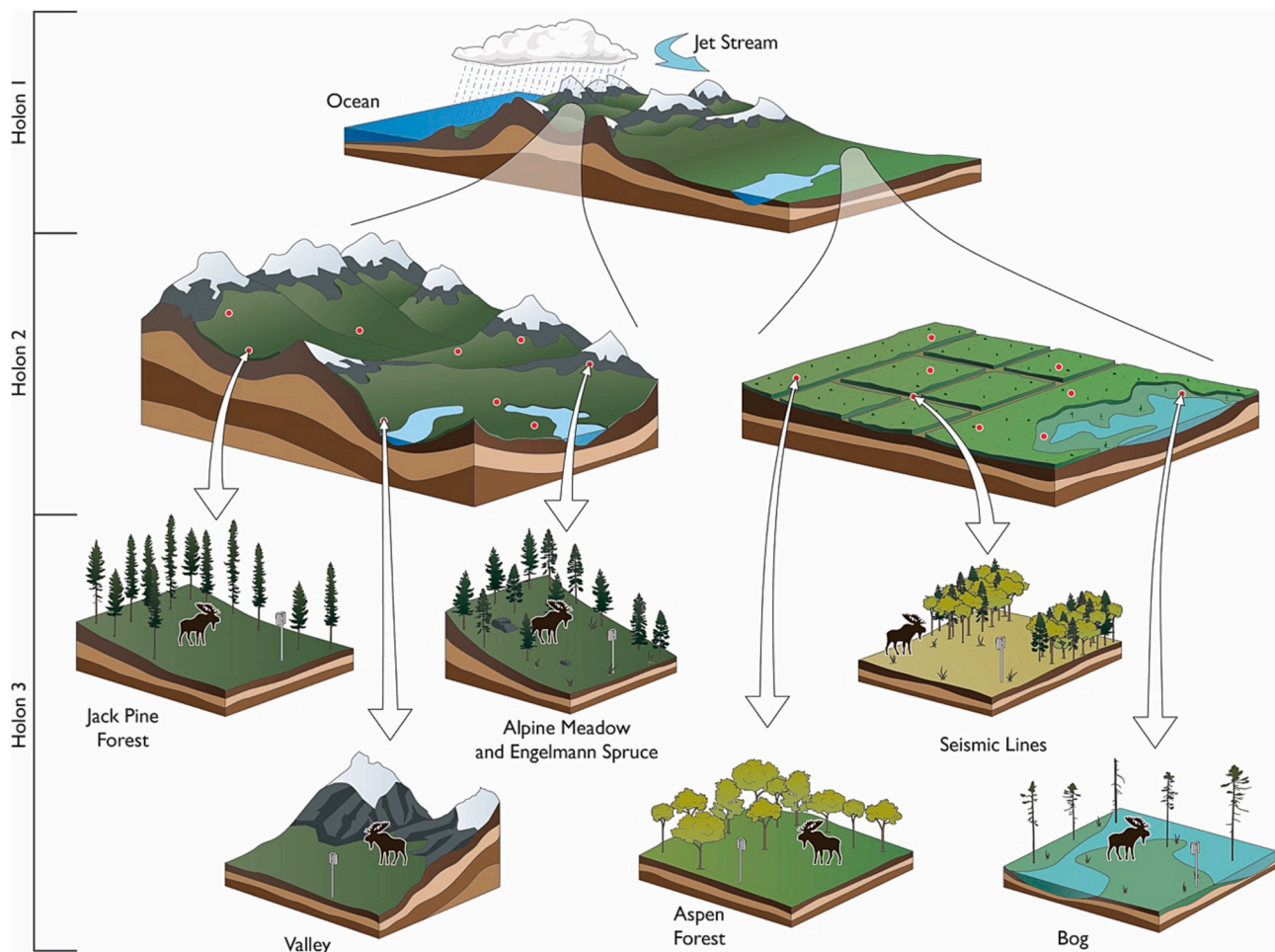
sites across 9 landscapes in Alberta from 2007 to 2020 and examined occurrence for 11 mammal species using generalized linear mixed models. White-tailed deer occurred more in higher disturbed sites within lower disturbed landscapes ( $\beta = -0.30 [-0.4 \text{ to } -0.15]$ ), whereas occurrence was greater in highly disturbed sites within highly disturbed landscapes for moose ( $\beta = 0.20 [0.09\text{--}0.31]$ ), coyote ( $\beta = 0.20 [0.08\text{--}0.26]$ ), and lynx ( $\beta = 0.20 [0.07\text{--}0.26]$ ). High disturbance sites in high productivity landscapes had higher occurrence of black bears ( $\beta = -0.20 [-0.46 \text{ to } -0.01]$ ), lynx ( $\beta = -0.70 [-0.97 \text{ to } -0.34]$ ), and wolves ( $\beta = -0.50 [-0.73 \text{ to } -0.21]$ ). Conversely, we found higher probability of occurrence in low productivity landscapes with increasing site disturbance for mule deer ( $\beta = 0.80 [0.39\text{--}1.14]$ ), and white-tailed deer ( $\beta = 0.20 [0.01\text{--}0.47]$ ). We found the ecological context created by aggregate sums (high overall landscape disturbance), and by subcontinental hydrogeological processes in which that landscape is embedded (high landscape productivity), alter mammalian responses to anthropogenic disturbance at local scales. These responses also vary by species, which has implications for large-scale conservation planning. Management interventions must consider large-scale geoclimatic processes and geographic location of a landscape when assessing wildlife responses to disturbance.

## 1. Introduction

Anthropogenic disturbance has led to a global decrease in terrestrial biodiversity, and landscape development is a primary driver of this phenomenon (Butchart et al., 2010; Maxwell et al., 2016). Mammals are especially at risk (Johnson et al., 2017) and anthropogenic stressors have been linked to behavioural changes in mammals though altered diel activity (Gaynor et al., 2018; Frey et al., 2020), population and community changes via altered predation rates (Rodewald et al., 2011; Neilson and Boutin, 2017; Boucher et al., 2022), and ultimately

geographic range reduction for many species (Laliberte and Ripple, 2004). Mitigating future biodiversity loss requires understanding and stopping the mechanisms leading to that loss; however, the processes underlying observed patterns of biodiversity declines are often unclear. 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 (Levin, 1992; Mazerolle and Villard, 1999; Levin, 2000; Steffan-Dewenter et al., 2002).

Theory to contextualize scale- and context-dependency, including



**Fig. 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 IIs are landscapes nested within that region wherein resources are variable, but processes are self-similar within, but different among. Holon IIIs are the areas around camera sites, e.g., a 1000 m<sup>2</sup> radius, wherein resources are proximal but variable and animals select those resources from choices distributed across the H<sup>II</sup> landscape. H<sup>I</sup> is built from H<sup>II</sup>s which are built from H<sup>III</sup>s. In turn H<sup>I</sup> processes constrain and entrain H<sup>II</sup> processes, which do the same for H<sup>III</sup> processes.

Wiens (1989) 'domains of scale' and hierarchy theory, offer an elegant way of conceiving nestedness and complexity in ecological systems (King, 1997). 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 (Allen and Hoekstra, 2015; Allen and Starr, 2017). 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  $H^{III}$  (Allen and Starr, 2017). Therefore, differences in ecological processes between multiple locations can potentially be explained by their existence within different holons. For example, within individual landscapes, animal responses to natural variability and anthropogenic disturbance at sampling locations are constrained by the landscape features and available resources within the greater landscape (Aebischer et al., 1993; Avgar et al., 2020). Thus, quantifying the features of those  $H^{II}$  landscapes should explain some variability in mammals' response to features across the multiple  $H^{III}$  of which they are composed. It therefore follows that in using a macro-ecological lens in the context of wildlife research (Beck et al., 2012; Leitão et al., 2019), smaller-scale sampling locations can be considered lower-order holons ( $H^{III}$ ), while landscapes within which those samples are collected can be considered as higher-order holons ( $H^{II}$ , Fig. 1) – themselves nested into a subcontinental, biogeographic system  $H^I$ .

The mediating effect of landscape traits on local species-habitat relationships is conceptually straight-forward but has been historically difficult to quantify for large animals, requiring repeatable data collection over vast areas. Indeed, populations of the same species can vary in the magnitude of responses or even show contrasting responses to anthropogenic disturbance in different study areas, making generalizable differences difficult (Fidino et al., 2021). 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 (Maris et al., 2018). Fortunately, the advent of camera trap technology for wildlife surveys (Burton et al., 2015; Caravaggi et al., 2017) allows investigating multiple research landscapes, scaled-up into a sampling network (Steenweg et al., 2017), to sample mammals at point locations ( $H^{III}$ ) clustered into discrete landscapes ( $H^{II}$ ).

Here, we pool data from camera trap surveys 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. This region holds the world's third largest oil deposit and has seen intense anthropogenic development for forest harvest, petroleum extraction, transportation, and recreation, leading to complex responses across the wildlife community (Boutin et al., 2012; Dickie et al., 2017; Fisher and Burton, 2018; Heim et al., 2019; Ladle et al., 2019; Mahon et al., 2019; Stewart et al., 2019a; Tattersall et al., 2020; Fisher et al., 2021; Fisher and Ladle, 2022; Roberts et al., 2022). Our hypotheses are built around two primary and well-established hypotheses about mammalian responses to disturbance in these areas: 1) though woodland caribou (*Rangifer tarandus*) are declining due to disturbance, many anthropophilic herbivores exploit the early-succession forage subsidies produced when mature forest is removed for timber or energy (MacDonald et al., 2020; Finnegan et al., 2021; Fuller et al., 2022), and 2) carnivores exploit these aggregations of prey (Boucher et al., 2022; McKay and Finnegan, 2022), as well as the movement subsidies offered by cleared linear features such as roads and seismic lines (McKenzie et al., 2012; Dickie et al., 2017). Given this, we predict herbivores' will be more likely to occur in areas of high anthropogenic features within 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, we

predict carnivores will also select habitats with higher anthropogenic features within high-productivity landscapes. We hypothesize the anthropophilic herbivores' selection for local site-level anthropogenic disturbance will be reduced in high-disturbance landscapes. In landscapes saturated by disturbance, the selection for any anthropogenic feature will be weak as there are many such anthropogenic features 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 aggregation of prey at rarer anthropogenic features in low-disturbance landscapes will produce a stronger carnivore response than in saturated high-disturbance landscapes.

## 2. Material and methods

### 2.1. Study areas

We studied nine landscapes spanning the western Nearctic boreal in Alberta, Canada. Here the Western Cordillera exerts a profound effect: moist Pacific Ocean air pulled eastward by Coriolis force mixes with cold Jet Stream air directed south by the Cordillera. Air masses are alternately adiabatically cooled and warmed over the mountains and adjacent boreal plain, distributing water heterogeneously over a variable edaphic substrate ( $H^I$ , Fig. 1). Together these processes induce differences in natural landcover, disturbances, and plant productivity (Schoennagel et al., 2004; Ireson et al., 2015). We sample this vast expanse in the Rocky Mountain east slopes (Willmore Wilderness, Yellowhead, Bighorn, and Kananaskis), central Alberta boreal-aspen mixed parkland (Beaverhills Biosphere), and the northern boreal forest (Whitefish Lake, Christina Lake, Richardson Backcountry, and Algar landscape) (Fig. S1). Landscapes varied with respect to area, and land-cover composition, productivity, and magnitude of anthropogenic disturbances (see further details below and Table S1, Fig. S1).

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 to facilitate independent sampling. Within those units a camera was placed on an active wildlife trail or linear feature 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). Cameras in three arrays were baited (Table S1). Cameras were programmed to take a photo (or a series of photos) when movement was detected by the infrared sensor with high sensitivity and fast trigger speed, and the date ranges of operability was determined based off timelapse photos or last photos taken if timelapse was not available (Table S1).

### 2.2. Quantifying landscape traits ( $H^{II}$ ) 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. We derived anthropogenic features from the Alberta Biodiversity Monitoring Institute (ABMI) Human Footprint Inventory (ABMI, 2010a, 2014, 2018), using the temporally closest dataset to camera sampling for each landscape. Around each camera site we calculated the proportion of area, within a 1-km radius buffer (sensu Fisher et al. (2011)), occupied by 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 the proportion area within the 1-km buffer these anthropogenic features occupied, but physically overlapping features or errors between datasets can potentially create values  $>1$ , thus this score is not a true proportion. For



each landscape ( $H^{\text{II}}$ ) we then created an overall landscape disturbance score by calculating the mean site disturbance among camera sites within that array. We do not account for natural disturbance regimes in this study and assume camera site locations are a representative sample of their respective landscapes (Fig. S2). Although the spatial scale (buffer size) at which habitat best explains a species' distribution varies among species (Fisher et al., 2011) we retained a consistent 1-km buffer as a mean of those buffer sizes, and a reasonable approximation representing resources available to wildlife at camera sites, without being biased by variable habitats at small-scales (e.g., 250 m), and avoiding overlap information between adjacent sites at large-scales (e.g., 5000 m). Importantly, previous work has shown little difference in estimated parameters due to small differences in buffer sizes (Toews et al., 2017).

Relationships between mammals and disturbance are amply evidenced but less so for productivity, especially carnivores. Ergo we quantified landscape ( $H^{\text{II}}$ ) productivity by classifying individual landscapes into bins of "higher" (> 50 % quantile) or "lower" (< 50 % quantile) summer plant productivity based on integrated Natural Vegetation Difference Index (NDVI, Fig. S3) using package *MODISvsp* (Busetto and Ranghetti, 2016). We elected to treat productivity as categorical as initial explorations using continuous NDVI values led to inflated errors and convergence issues. Note our metric is not objective "high" or "low" productivity, but rather comparatively "higher" or "lower" within our sample of camera arrays (Fig. S3).

To control for variance in mammal occurrence due to non-focal factors, we considered natural vegetation (forest) heterogeneity, snow cover, seasonality, and topography. We quantified natural landscape features around camera sites within the 1-km radius buffer around each camera site. We used the (ABMI) Wall-to-Wall Land cover dataset (ABMI, 2010b) to extract each buffer's proportion water, shrub, grassland, conifer, broadleaf, and mixed landcover types. 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. Since attractants are known to influence species detections (Holinda et al. (2020), but see also Stewart et al. (2019b)) we also included a categorical variable for whether camera sites were baited (see model descriptions below).

### 2.3. Mammal site-use

Camera images were identified to species using Timelapse Image Analyzer 1.0 and 2.0 (Greenberg et al., 2019) or Camelot (Hendry and Mann, 2017). 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. Events were considered independent if images of the same species, at the same site, were taken  $\geq 30$  min apart. This filtering process led us to consider 11 species: black bear (*Ursus americanus*), caribou, 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*). We discretized species detections into weekly presence/absence at each site (Fig. S4), which can be interpreted as relative abundance or frequency of site-use over the entire sampling period for a given site.

### 2.4. Statistical analysis

We used package *corrplot* (Wei et al., 2017) 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 (Fig. S5, Table S2).

We considered a non-detection to represent a true zero, as each species has the opportunity to occupancy a site within a week if it chooses. Thus we considered the 0 s in each site's repeat detection data as due to temporary emigration, a part of the site-choice state process (Efford and Dawson, 2012; Neilson et al., 2018; Stewart et al., 2018), rather than a false absence derived from the observation process sensu (MacKenzie et al., 2017). Moreover, weekly sampling at the same site would reduce the probability of false absences to zero. We constructed a separate generalized linear mixed model (GLMM) for each species examining weekly presence as a binomial response (Eq. (1), notation following (Zuur and Ieno, 2016)). The mediating influence of landscape traits on camera-site/mammal relationships was investigated by interacting  $H^{\text{III}}$  site disturbance  $\times H^{\text{II}}$  landscape disturbance, and  $H^{\text{III}}$  site disturbance  $\times H^{\text{II}}$  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 (across the entire range of values, rather than array specific) to facilitate comparisons between estimated model coefficients and improve computational efficiency. *Weekly Species Presence<sub>ij</sub>* is the  $i^{\text{th}}$  observation at Site  $j$ , where Site ID is a random intercept with  $j^{\text{th}}$  level  $j$  = individual site. Categorical variables included landscape productivity (where  $k^{\text{th}}$  level  $k$  = lower or higher), season (where  $l^{\text{th}}$  level  $l$  = no snow season or snow season), baited (where  $m^{\text{th}}$  level  $m$  = baited camera or not baited camera). We tested for statistically significant improvement of model fit with the Site ID random effect structure using likelihood ratio tests (Bolker et al., 2009). Note nested random effects of Site ID within Array ID were tested in early stages of model development, but this resulted in model convergence issues as a result of the singular values of Landscape Disturbance for each Array, so we proceeded with only Site ID. All models assumed a binomial distribution with a logit link function, and were fit with package *glmmTMB* (Magnusson et al., 2017) using restricted maximum likelihood.

$$\begin{aligned} \eta_{ijklm} = & \beta_0 + \beta_1 \text{Site Disturbance}_{ij} \times \text{Landscape Disturbance}_{ij} \\ & + \beta_2 \text{Site Disturbance}_{ij} \times \text{Landscape Productivity}_{ijk} \\ & + \beta_3 \text{Site Disturbance}_{ij} + \beta_4 \text{Landscape Disturbance}_{ij} \\ & + \text{Landscape Productivity}_{ijk} + \beta_5 \text{Water}_{ij} + \beta_6 \text{Shrub}_{ij} + \beta_7 \text{Grass}_{ij} \\ & + \beta_8 \text{Broadleaf}_{ij} + \beta_9 \text{Mixed}_{ij} + \beta_{10} \text{TRI}_{ij} + \beta_{11} \text{Snow}_{ij} + \text{Season}_{ijl} \\ & + \text{Baited}_{ijm} + \text{Site ID}_j \end{aligned} \quad (1)$$

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

$$\text{Weekly Species Presence}_{ij} \sim \text{Bernoulli}(\pi_{ijklm})$$

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

We calculated variance inflation factors (VIFs) for each model term separately for each species using package *performance* (Lüdtke et al., 2021), 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* (Lüdtke, 2018). We considered estimates of fixed effects to be "significant" when 95 % confidence intervals did not overlap zero.  $\beta$  coefficient estimates are reported as mean and 95 % confidence interval range. All data manipulation and statistical analyses were done using R-Studio v4.2.3 (R Core Team, 2017).

## 3. Results

Across these diverse northwestern Nearctic landscapes, we detected

42 mammal species from nine camera arrays from 2007 to 2020. The most frequently detected wildlife species were white-tailed deer, black bear, and moose, while the least frequently detected were American badger (*Taxidea taxus*), bushy-tailed woodrat (*Neotoma cinerea*), and muskrat (*Ondatra zibethicus*) (Table S3). We collected images from 957 sites, representing 380,635 camera trap days. The random effect structure of Site ID significantly improved model fit for all species (Table S5). We removed model terms for local site disturbance for caribou, cougar, coyote, lynx, and wolves due to inflated VIF values (Table S6), thus omitting those species when making model predictions (see below).

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

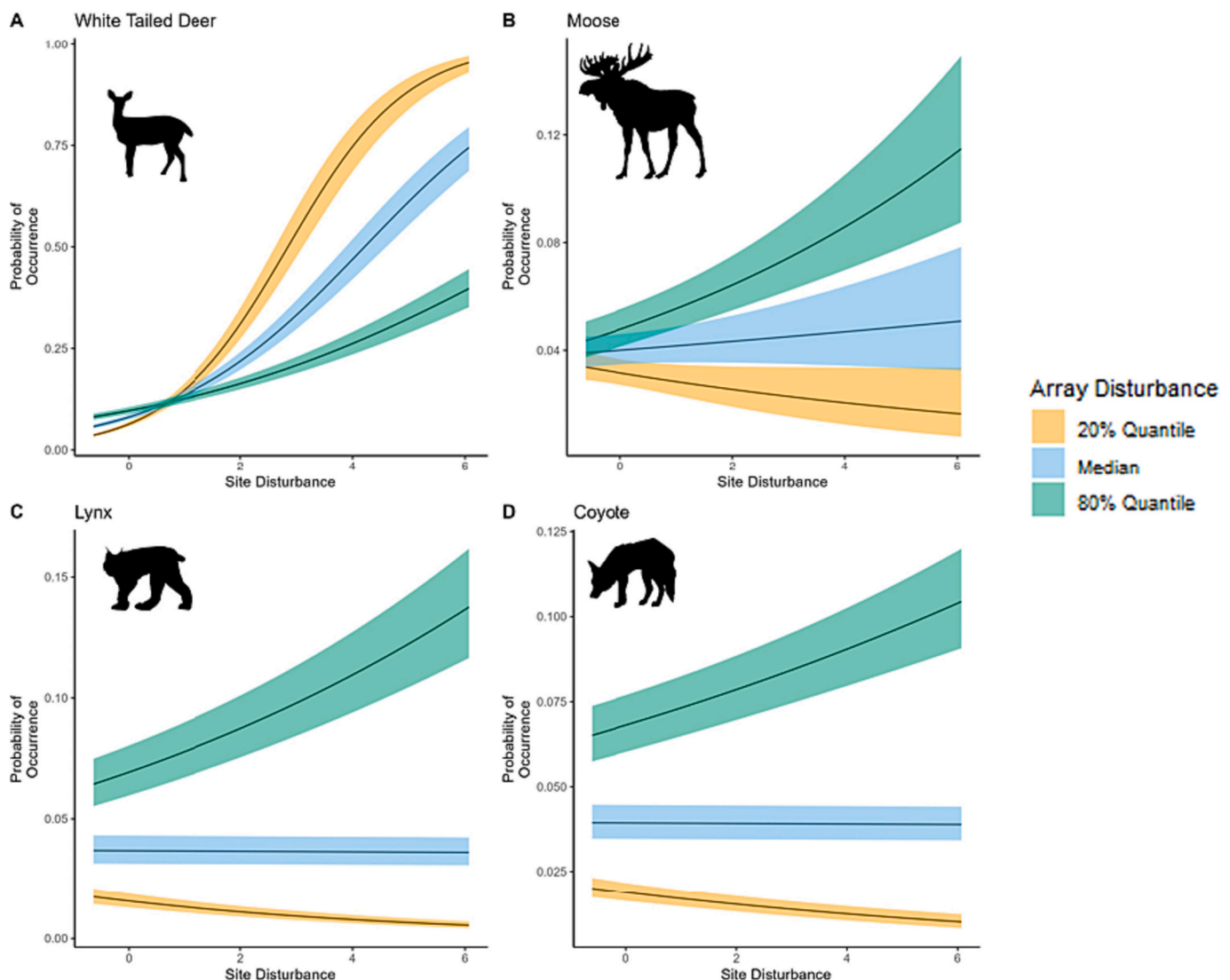
Landscape-level disturbance was statistically significant for all species. Higher landscape disturbance led to a significant higher probability of occurrence for all species except black bears ( $\beta = -0.3$  [−0.42 to −0.17]) and caribou ( $\beta = -1.7$  [−2.2 to −1.21]), although predicted changes in probability of occurrence were small across the range of array disturbance values for cougars, elk, grizzly bear, moose, and mule deer (Fig. 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. We failed to find a statistically significant effect of site disturbance elk, grizzly bear, moose, or mule deer (reminding readers we omitted several species here due to VIFs, Table S3).

The interaction between site and landscape-scale disturbance was statistically significant for four species (two predators and two prey), providing support that use of locally disturbed sites varies within the context of landscape-scale disturbance. White-tailed deer were more likely to occur in more highly disturbed sites within less disturbed landscapes ( $\beta = -0.30$  [−0.4 to −0.15], Fig. 2A), whereas occurrence was greater in highly disturbed sites within highly disturbed landscapes for moose ( $\beta = 0.20$  [0.09–0.31], Fig. 2B), coyote ( $\beta = 0.20$  [0.08–0.26], Fig. 2C), and lynx ( $\beta = 0.20$  [0.07–0.26], Fig. 2D). For model predictions for all species and accompanying 95 % confidence intervals see Fig. S7.

### 3.2. 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 had



**Fig. 2.** Mean probability scale model predictions for weekly occurrence of species with significant interaction terms for scaled site disturbance and scaled landscape disturbance A) White Tailed Deer, B) Moose, C) Lynx, and D) Coyote. Note different scales for each species. See supplemental materials for estimates for complete species set.

higher weekly site use in lower productivity landscapes (Table S4). However, predicted changes in weekly occurrence between lower and higher productivity landscapes alone were minimal (Fig. S8). Model predictions for the interaction between site disturbance and landscape productivity showed a much stronger effect for some species (Fig. S9). High disturbance sites in high productivity landscapes were preferred by black bears ( $\beta = -0.20$  [-0.46 to -0.01], Fig. 3A), lynx ( $\beta = -0.70$  [-0.97 to -0.34], Fig. 3B), and wolves ( $\beta = -0.50$  [-0.73 to -0.21], Fig. 3C). Conversely, this relationship was opposite for mule deer ( $\beta = 0.80$  [0.39–1.14], Fig. 3D), and white-tailed deer ( $\beta = 0.20$  [0.01–0.47], Fig. 3E), which had a higher probability of occurrence in low productivity landscapes with increasing site disturbance. So, while there is some support for our hypotheses regarding carnivore aggregation at disturbed sites in disturbed landscapes, we found the opposite expected relationship with some herbivore species through aggregation at high disturbance sites in low productivity landscapes. However, we still found a high probability of occurrence for these herbivores in disturbed sites within disturbed landscapes, lending support for the proposed mechanism.

The effects of the controlling variables and interaction terms of interest were variable between species (Table S4). Unsurprisingly, season was a statistically significant fixed effect for all species, whereas other fixed effects were only variably important for some species (Table S4).

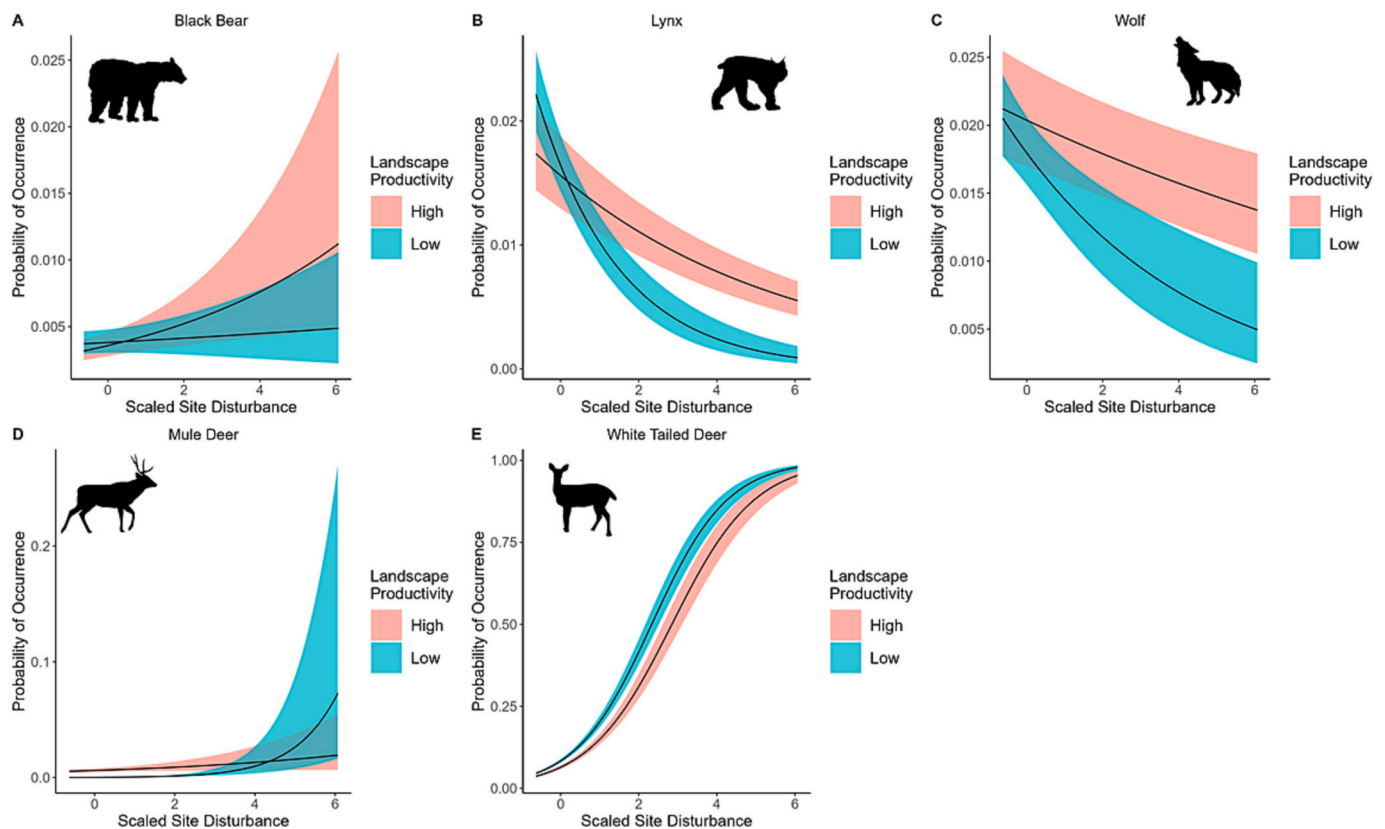
#### 4. Discussion

Ecological processes occurring at sub-continental scales produce landscapes that vary in productivity and disturbance. In the north-western Nearctic 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 (King, 1997; Allen and Starr, 2017) which posits that self-similar, large-scale holons  $H^I$  entrain processes occurring at medium-scale nested landscape-level holons  $H^{II}$ , which in turn entrain processes at nested small-scale holons  $H^{III}$  (Fig. 1). In ecologically meaningful terms, although boreal forest landscapes ca. 3000 km<sup>2</sup> in size are de facto composites of 3000, 1-km<sup>2</sup> parts, they are more than the sum of those parts. Here, we found that the ecological context created by that aggregate sum (high overall landscape disturbance), and by the sub-continental hydrogeological processes in which that landscape is embedded (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 variability is a fundamental goal of ecology, and we anticipate species responses follow some general laws; so far, these are rare (Lawton, 1999). Instead we ascribe wide variations in species-habitat relationships (e.g. Fisher et al., 2005) into the bin of context-dependency and the 'pattern and problem of scale' (Levin, 1992), with the mechanisms behind this dependency hypothesized (Holling, 1992) 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 across 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



**Fig. 3.** Mean probability scale model predictions ( $\pm$  95 % CIs) for weekly occurrence species with a significant interaction term for scaled site disturbance and categorical landscape productivity A) Black bear, B) Lynx, C) Wolf, D) Mule Deer, E) White-Tailed Deer. Note different Y-axis scales for each species. See supplemental materials for estimates of complete species set.

costs (Schneider et al., 2010; Hebblewhite, 2017). As restoration success itself is known to be context-dependent (Kouki et al., 2012), our hierarchical macroecological approach presents a framework that 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 (Boutin et al., 2012; Serrouya et al., 2015; Serrouya et al., 2017), as opposed to spending conservation effort in high-disturbance but low productivity landscapes where predator responses are less strong. Using data from multiple sites also generates new questions on species responses at different scales. For example, black bears in the Algar landscape are less likely to use sites with higher disturbance (Tattersall et al., 2020), but we found the opposite where black bears preferred increasing disturbance. Although we did not examine specific disturbance types here, future investigation may be required to understand site-specific responses for black bears, or other species if similar conflicting findings present themselves. 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 (Aronson et al., 2020; Meli et al., 2022).

We found that landscape-scale disturbance was generally a more important driver of species detection than site-scale disturbance, and we offer two possible explanations for this. First, higher disturbance provides early-succession forage subsidies, increasing anthrophilic herbivore populations and subsequently the predators of those species (Latham et al., 2011). Therefore landscapes with overall higher disturbance (up to some threshold) may simply have larger populations of certain species, and thus are more available for detection. This is supported by our findings of higher productivity landscapes generally showing greater detections, but this was not consistent for all species. Second, landscapes with greater overall disturbance likely contain more linear features which offer movement subsidies for some species (Dickie et al., 2017), and greater movement throughout the landscape would translate to higher numbers of species detections (Neilson et al., 2018; Stewart et al., 2018).

#### 4.1. 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 we did not and could not apply a probabilistic sampling design to  $H^1$ , the subcontinental region. Stratifying  $H^1$  by disturbance and productivity would be a desired approach; for example, undisturbed landscapes are logistically harder to sample and unfortunately underrepresented in our analysis. We advocate again for a macroecological and ultimately global camera-based biodiversity network (Steenweg et al., 2017) with landscapes allocated to strata “treatments” as coordinated distributed experiments (Fraser et al., 2013). 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. However, given that management decisions are not made at global scales, we recognize that regional-specific projects will inevitably be prioritized for informing conservation actions by regional (provincial/state) and federal bodies. Further, arrays were sampled in different years (Table S1), and we were unable to account for temporal variation in this synthesis. Ideally, future coordinated sampling will take place across multiple landscapes in the same years. 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 for many effects, which contrasts prior studies that do show significant effects. 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., 2021; Stewart et al., 2019a; Heim et al., 2019; Fisher and Burton, 2018). This demonstrates the common “scale problem” of biology (Levin, 1992): 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. (Suraci et al., 2021; Sévêque et al., 2022), 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. Furthermore, different analytic approaches to examinations of wildlife responses such as modeling nonlinear relationships (sensu Suraci et al., 2021) or structural equation modeling to examine causal pathways, may yield alternative findings that should be considered alongside our approach here.

## 5. Conclusions

The recent call for integrated camera-monitoring networks at broad spatial scales (Steenweg et al., 2017) to ask questions about generalizable macroecological laws (Lawton, 1999) has begun to be answered by research examining wildlife responses to anthropogenic stressors across multiple landscapes (Rich et al., 2017; Zimova et al., 2020; Fidino et al., 2021; Magle et al., 2021; Suraci et al., 2021; Chen et al., 2022). These collaborative approaches are advantageous as they avoid erroneously extrapolating findings from single focal populations to adjacent, potentially dissimilar 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 (Aronson et al., 2016; Magle et al., 2021). Indeed, populations of the same species can vary in the magnitude of responses or even show contrasting responses to anthropogenic disturbance (Fidino et al., 2021). 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.

## CRedit authorship contribution statement

**Andrew F. Barnas:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. **Andrew Ladle:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Software, Visualization, Writing – original draft, Writing – review & editing. **Joanna M. Bugar:** Conceptualization, Data curation, Investigation, Resources, Writing – review & editing, Funding acquisition. **A. Cole Burton:** Conceptualization, Data curation, Funding acquisition, Investigation, Resources, Writing – review & editing. **Mark S. Boyce:** Data curation, Funding acquisition, Investigation, Resources, Writing – review & editing. **Laura Eliuk:** Data curation, Investigation, Resources, Writing – review & editing. **Fabian Grey:** Data curation, Funding acquisition, Investigation, Resources, Writing – review & editing. **Nicole Heim:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Software, Validation, Visualization, Writing – original draft, Writing –



review & editing. **John Paczkowski:** Data curation, Funding acquisition, Investigation, Resources, Writing – review & editing. **Frances E.C. Stewart:** Data curation, Funding acquisition, Investigation, Resources, Writing – review & editing. **Erin Tattersall:** Data curation, Investigation, Resources, Writing – review & editing. **Jason T. Fisher:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. Funding for this synthesis was provided by the Oil Sands Monitoring Program; this does not represent the views of the program.

## Data availability

All data will be made publicly available at Borealisdata.ca

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.169285>.

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