Industrial landscape changes alter fine-scale mammal diversity and mammalian predator–prey dynamics in the northwest Nearctic

by

Macgregor Aubertin-Young
B.Sc. (Honours), University of British Columbia, 2019

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We acknowledge and respect the lək̓ʷəŋən peoples on whose traditional territory the university stands and the Songhees, Esquimalt and W̱SÁNEĆ peoples whose historical relationships with the land continue to this day.

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ABSTRACT

Biodiversity has been heavily impacted by anthropogenic landscape changes associated with natural resource extraction. Terrestrial mammals, which disproportionately maintain ecosystem functions, are among the species most affected by anthropogenic landscape changes. In turn, it is important that we incorporate mammal conservation into natural resource extraction to mitigate biodiversity change, for which we must better understand the dynamics of mammal communities. I used data from motion-activated camera traps deployed in the northwest Nearctic to investigate two aspects of mammal communities: how the environment shapes fine-scale mammal diversity and how mammalian predator species coexist. In my first study, I compared how well natural and anthropogenic landscape features explain fine-scale mammal diversity within and between six variably industrialized landscapes. I found that anthropogenic landscape features explain fine-scale mammal diversity better than natural features in heavily industrialized landscapes, where they may increase or decrease diversity. In my second study, I examined whether prey partitioning facilitates the coexistence of mammalian predator species in an industrialized boreal landscape. My findings suggest that sympatric predator species only partially partition prey, as some predator species had identical prey associations. Strikingly, though, I also found that all predators were positively associated with white-tailed deer, an invasive prey species made abundant by industrial landscape changes. Together, these findings reveal that industrial landscape changes significantly alter both the spatial distributions and predator–prey dynamics of mammal communities. This work can inform conservation and restoration strategies for slowing biodiversity change.

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DEDICATION

I dedicate this work to Papa, who brought me into nature and taught me the value of knowledge.

Chapter 1

Introduction

Biodiversity has been heavily impacted by anthropogenic activities, causing biodiversity loss, altered ecosystem functioning, and novel species interactions (Foley et al., 2005; Maxwell et al., 2016). Of the many activities contributing to biodiversity change, anthropogenic landscape changes from natural resource extraction have contributed majorly (Maxwell et al., 2016). Although biodiversity would thus benefit from decreasing the intensity of natural resource extraction, natural resources sustain our socioeconomic systems and will likely be extracted more intensely in the coming decades (Hatfield-Dodds et al., 2017). It is therefore critical that we incorporate biodiversity conservation strategies into natural resource extraction, for which we must understand the ecological consequences of industrial landscape changes (Tilman et al., 2017).

By removing and fragmenting natural habitats, industrial landscape changes impact the distribution and abundance of numerous taxa (Newbold et al., 2015), many of which perform important ecosystem functions (Brose & Hillebrand, 2016). However, habitat loss and fragmentation most strongly impact large-bodied, slow-reproducing species, such as terrestrial mammals (Crooks et al., 2017; Keinath et al., 2017), which disproportionately maintain ecosystem functions (Lacher et al., 2019; Ripple & Beschta, 2012). Mammal conservation is thus integral to the broader conservation of biodiversity and should be a priority in mitigating the ecological impacts of industrial activities.

Industrial landscape changes affect mammals directly and indirectly (Tylianakis et al., 2008; Venier et al., 2014). Researchers have paid considerable attention to the direct effects, which most recognizably include species declines from the loss of critical habitats (Fahrig, 2001; Hebblewhite, 2017). Recently, though, much attention has turned to the indirect effects of industrial landscape changes (Cunningham et al., 2018; DeMars & Boutin, 2018; Serrouya et al., 2021), which arise through species interactions and implicate entire communities; changes in the distribution and abundance of one species often impact other species connected through competition, predation, or facilitation (Burgar et al., 2019; Ripple & Beschta, 2012; Tylianakis et al., 2008). It is important that we consider such indirect ecological effects in mammal conservation strategies because their omission may yield unexpected negative outcomes, such as declines in the species trying to be being conserved (Godsoe & Harmon, 2012; Tylianakis et al., 2008). Before we can effectively do so, however, we must better understand many aspects of mammal community dynamics.

One major deficiency in our understanding of mammal communities comes from uncertainty in how the environment shapes species diversity, particularly at small spatial scales (Field et al., 2009). Researchers have long sought environmental determinants of species diversity to explain species diversity gradients and advance the field of biogeography (Whittaker, 1972). Contextualized in mammal conservation, understanding the environmental determinants of species diversity may help predict where species are likely to occur and interact across complex landscapes. Knowledge on where species occur and interact may then be used to design and implement effective conservation and restoration measures.

Another deficiency in our understanding of mammal communities comes from uncertainty in how multiple species coexist (Valladares et al., 2015). This topic extends from niche theory and the competitive exclusion principle, which states that multiple species using identical resources cannot coexist due to resource competition (Amarasekare, 2003). By the competitive exclusion principle, it is likely, and hence widely assumed, that mammal species coexist by partitioning resources (Schoener, 1974). Yet, it remains unclear which resources are partitioned, and how strongly resources are partitioned, in many mammal communities. Uncertainty in how species use and partition resources obscures the strength of species interactions and thus impedes predictions of how industrial landscape changes will indirectly alter mammal communities.

Aiming to resolve these deficiencies, I conduct two studies using motion-activated camera traps to investigate the environmental determinants of fine-scale mammal diversity (Chapter 2) and the mechanisms by which mammalian predator species coexist (Chapter 3). My primary intention is to advance ecological theory, but in a way that allows species interactions and community dynamics to be better incorporated into conservation and restoration strategies. Accordingly, I focus on mammal communities in Alberta, Canada, which have been majorly affected by industrial landscape changes (Fisher & Burton, 2018).

To understand environmental determinants of species diversity, I compare how well natural and anthropogenic landscape features explain fine-scale mammal diversity within and between six variably industrialized landscapes. I also examine the direction and magnitude with which specific anthropogenic features alter fine-scale mammal diversity. I chose to compare the influence of natural and anthropogenic diversity determinants to weigh the ecological significance of anthropogenic determinants against that of natural processes. Understanding the influence of anthropogenic diversity determinants relative to natural determinants may help decision-makers determine which industrial features or industrialized landscapes to prioritize for conservation and restoration.

To understand how mammalian predator species coexist, I examine the spatial associations of different predator and prey species in an industrialized boreal forest landscape. More specifically, I compare species' spatial associations to test whether sympatric predator species coexist by partitioning prey species. I also investigate how white-tailed deer (*Odocoileus virgnianus*), an invasive prey species made abundant in many southern boreal landscapes by industrial landscape changes (Fisher & Burton, 2021), alter historical predator–prey interactions. I focus on the boreal biome because it contains a simple and well-studied mammal community (Krebs et al., 2001) in which species interactions can be feasibly studied across most of the community.

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Chapter 2

Anthropogenic landscape changes explain fine-scale mammal diversity better than natural factors in heavily industrialized landscapes

This chapter will be submitted for publication with coauthors Andrew Ladle, Joanna Burgar, A. Cole Burton, Nicole Heim, Fabian Grey, John Paczkowski, Eric Higgs, and Jason T. Fisher.

2.1 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 small spatial scales (i.e., < 1 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 diversity determinants (e.g., van Heezik et al., 2008), partially obscuring the ecological significance of anthropogenic diversity determinants. This has maintained uncertainty in how strongly anthropogenic diversity determinants rival natural diversity determinants, especially regarding terrestrial mammal diversity. Mammals are among the species most 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 an important 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, I 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 I did not predict which of the mechanisms (proportion or heterogeneity) would dominate. Second, I tested whether the proportion and heterogeneity of anthropogenic forest clearings increase mammalian alpha diversity, as predicted by the habitat heterogeneity and keystone structure hypotheses.

2.2 Methods

2.2.1 Study regions

I 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 fur (*Abies lasiocarpa*), and subalpine larch (*Laryx 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. I hereafter refer to the lowly industrialized mountain landscape as “LD-M” and highly industrialized mountain landscapes as “HD-M1” (Bighorn Backcountry) and “HD-M2” (Kananaskis Country), abbreviating their degree of industrialization 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. I ranked the degree of industrialization 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 (Appendix 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*).

2.2.2 Sampling design

I 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 (Appendix Table A2). As landscapes were sampled by different schedules and with the possibility of camera malfunctions, I 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 wildlife 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. Although the placement of cameras on wildlife trails may decrease the probability of detecting species that avoid wildlife trails (Hofmeester et al., 2021), I assumed that this potential influence did not bias the estimated strength of alpha diversity determinants. I describe the specific

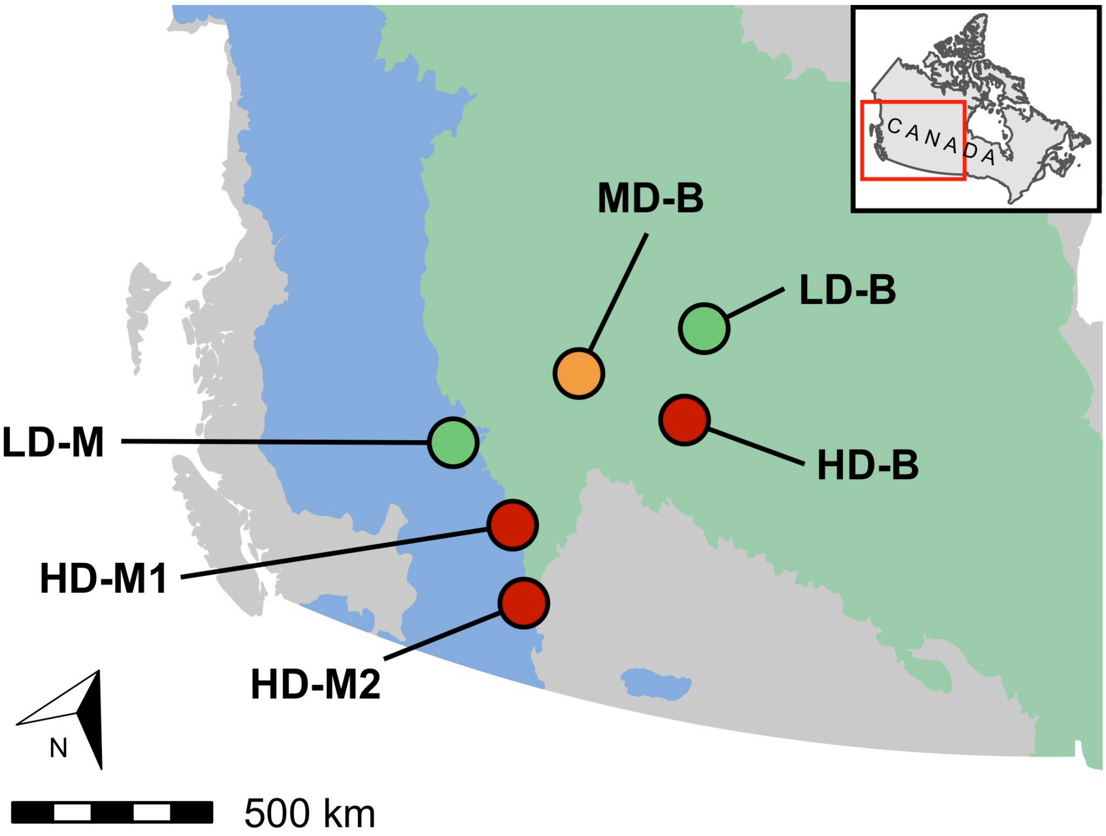

Figure 2.1. The location of landscapes in which camera traps were deployed to compare environmental determinants of mammalian alpha diversity. Landscapes spanned boreal (light green) and mountainous (blue) ecoregions and were either lowly (green circle), moderately (orange), or highly (red) industrialized. Ecoregional boundaries were obtained from the United States Environmental Protection Agency.

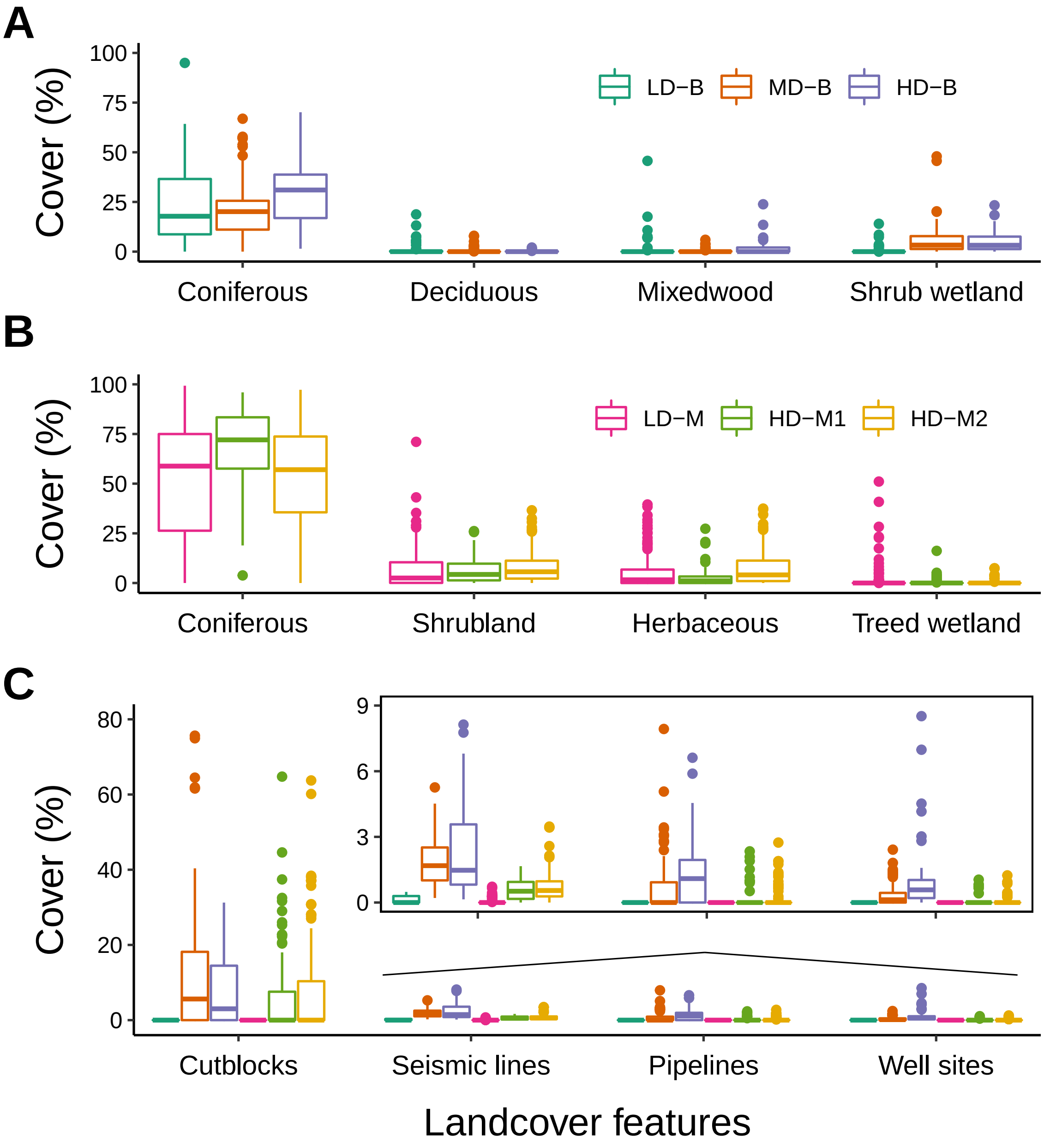

Figure 2.2. Boxplots of the proportional coverage of natural (A–B) and anthropogenic (C) landcover classes in six variably industrialized landscapes in the northwest Nearctic. The proportional coverage of each class was measured within 1 km of camera traps that were deployed across each landscape; each 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.

sampling designs for each landscape in Appendix Table A2.

2.2.3 Measuring alpha diversity

In each landscape, I calculated alpha diversity at individual camera sites (i.e., localities) by estimating the asymptotic species richness from species' site-level relative abundances, which I 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). I 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. I 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). I measured species' site-level relative abundance as the number of independent images of each species at each site, and I considered images of the same species to be independent if they were taken more than 1 hour apart.

I 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, I used two consecutive 30-day periods because of their shorter sampling durations. I 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 I intended to capture. I 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). I included all observed mammal species except bats and domestic livestock. I 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.

2.2.4 Natural and anthropogenic diversity determinants

I 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), I measured each feature using buffer radii of 250–2500m in 250m increments. I 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). I obtained MODIS-derived EVI values at 250m resolution using the R package *MODISTools* (Tuck et al., 2014), and following recommendations to improve data quality, I 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, I 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, I used the averaged EVI value from the previous period. To reduce collinearity between EVI and season, I standardized EVI within seasons separately (mean = 0, standard deviation = 1) such that EVI values represent the difference from the relevant seasonal mean.

As I wanted to compare natural and anthropogenic diversity determinants and test whether the proportions of anthropogenic features increased alpha diversity, I measured the proportions of four anthropogenic features and four natural habitats around each camera. I refer to these as potential keystone structures. To consider the most probable potential keystone structures, I 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, I 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 sometimes 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). I measured the proportion of anthropogenic features using the Alberta Biodiversity Monitoring Institute Human Footprint Inventory (Alberta Biodiversity Monitoring Institute, 2021) from the year nearest available to the sampling year in each landscape.

For natural keystone structures, I considered different habitats between the distinct mountain and boreal ecoregions. In boreal landscapes, I considered lowland spruce forest, lowland deciduous forest, lowland mixedwood forest, and shrub wetland, which I reclassified from the Alberta Vegetation Inventory (Nesby, 1997). In mountain landscapes, I considered coniferous forest, shrubland, herbaceous, and treed wetland, which I reclassified using a 16-class landcover dataset Nijland et al., 2015. I 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, I measured the coverage of these habitats from the year nearest available to the sampling year in each landscape.

I 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, I 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.

2.2.5 Modelling: Spatial scale and model selection

I 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 each represented by four covariates (proportions of potential keystone structures). To compare the maximum support for each of these models in each landscape, I first found the best-supported spatial scale at which each covariate explained mammalian alpha diversity in each landscape. To do this, I 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). I included season and season–covariate interactions as fixed predictors in each of these models to account for potential season-dependent relationships (Schooley 1994), and I included camera site as a random intercept to account for repeated alpha diversity measurements at each camera (Zuur et al. 2009). I used summer as the reference level for interaction terms. I 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, I used model selection to compare how well each model (i.e. diversity determinant measured at the best-supported spatial scale) explained alpha diversity in each landscape. I could not compare anthropogenic diversity determinants in the lowly

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 Inventory.

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

industrialized landscapes (LD-M and LD-B) because the proportions of anthropogenic features were too low for model convergence, leaving comparisons between only the natural diversity determinants. In this step, I 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. I considered models with < 2 ΔAIC to have the highest support, and I used 10-fold cross-validation to assess model fit (Roberts et al., 2017). While interpreting these models, I considered β estimates to be significantly different from zero if the 95% confidence interval did not overlap zero. I standardized model covariates (mean = 0, standard deviation = 1) within each landscape and ensured that none were highly collinear ($r < 0.7$).

2.3 Results

2.3.1 Anthropogenic diversity determinants outweighed natural diversity determinants in highly industrialized landscapes

Anthropogenic landscape features explained mammalian alpha diversity better than productivity, habitat heterogeneity, and natural keystone structures in each highly industrialized 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 industrialized 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 industrialized landscapes.

2.3.2 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 industrialized 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 industrialized boreal landscape (MD-B: $\beta_{\text{Well}} = 0.14 \pm 0.22$, $p = 0.207$). The relationship between alpha diversity and the proportion of well sites did not change between seasons in three of four industrialized landscapes (HD-M1: $\beta_{\text{Well:Season}} = 0.19 \pm 0.47$, $p = 0.425$; MD-B: $\beta_{\text{Well:Season}} = 0.20 \pm 0.38$, $p = 0.303$; HD-B: $\beta_{\text{Well:Season}} = –0.06 \pm 0.11$, $p = 0.257$), but weakened in winter in the other (HD-M2: $\beta_{\text{Well:Season}} = –0.60 \pm 0.39$, $p = 0.002$).

Alpha diversity decreased with the proportion of seismic lines and cutblocks in both industrialized 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: $\beta_{\text{Seismic:Season}} = 0.10 \pm 0.25$, $p = 0.435$; $\beta_{\text{Cutblock:Season}} = 0.10 \pm 0.32$, $p = 0.532$; HD-B: $\beta_{\text{Seismic:Season}} = 0.19 \pm 0.20$, $p = 0.062$; $\beta_{\text{Cutblock:Season}} = 0.12 \pm 0.11$, $p = 0.062$). 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 2.4). This relationship did not change between seasons ($\beta_{\text{Anthropogenic heterogeneity:Season}} = -0.12 \pm 0.13$, $p = 0.059$). Alpha diversity was unaffected by anthropogenic heterogeneity in the three other industrialized 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 2.2. 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; $AICc_w$ is the AICc weight. LL is the log-likelihood. RMSE is the root mean-squared error from 10-fold cross-validation.

LS	Hypothesis	*k*	ΔAICc	$AICc_w$	LL	RMSE
LD-M	**Productivity**	**7**	**0.00**	**1.00**	**-737.10**	**2.51**
	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
HD-M1	**Anthropogenic keystone structures**	**13**	**0.00**	**0.76**	**-608.47**	**1.56**
	Natural keystone structures	13	3.46	0.14	-610.20	1.59
	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
HD-M2	**Anthropogenic heterogeneity**	**7**	**0.00**	**0.82**	**-1053.71**	**2.38**
	Anthropogenic keystone structures	13	3.23	0.16	-1049.07	2.38
	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

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; $AICc_w$ is the AICc weight; LL is the log-likelihood RMSE is the root mean-squared error from 10-fold cross-validation.

LS	Hypothesis	*k*	ΔAICc	$AICc_w$	LL	RMSE
LD-B	**Productivity**	**7**	**0.00**	**0.67**	**-358.19**	**0.98**
	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
MD-B	**Natural keystone structures**	**13**	**0.00**	**0.94**	**-632.90**	**1.32**
	Productivity	7	7.20	0.03	-642.80	1.33
	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
HD-B	**Anthropogenic keystone structures**	**13**	**0.00**	**0.98**	**-540.10**	**1.50**
	Natural heterogeneity	7	8.59	0.01	-550.81	1.54
	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

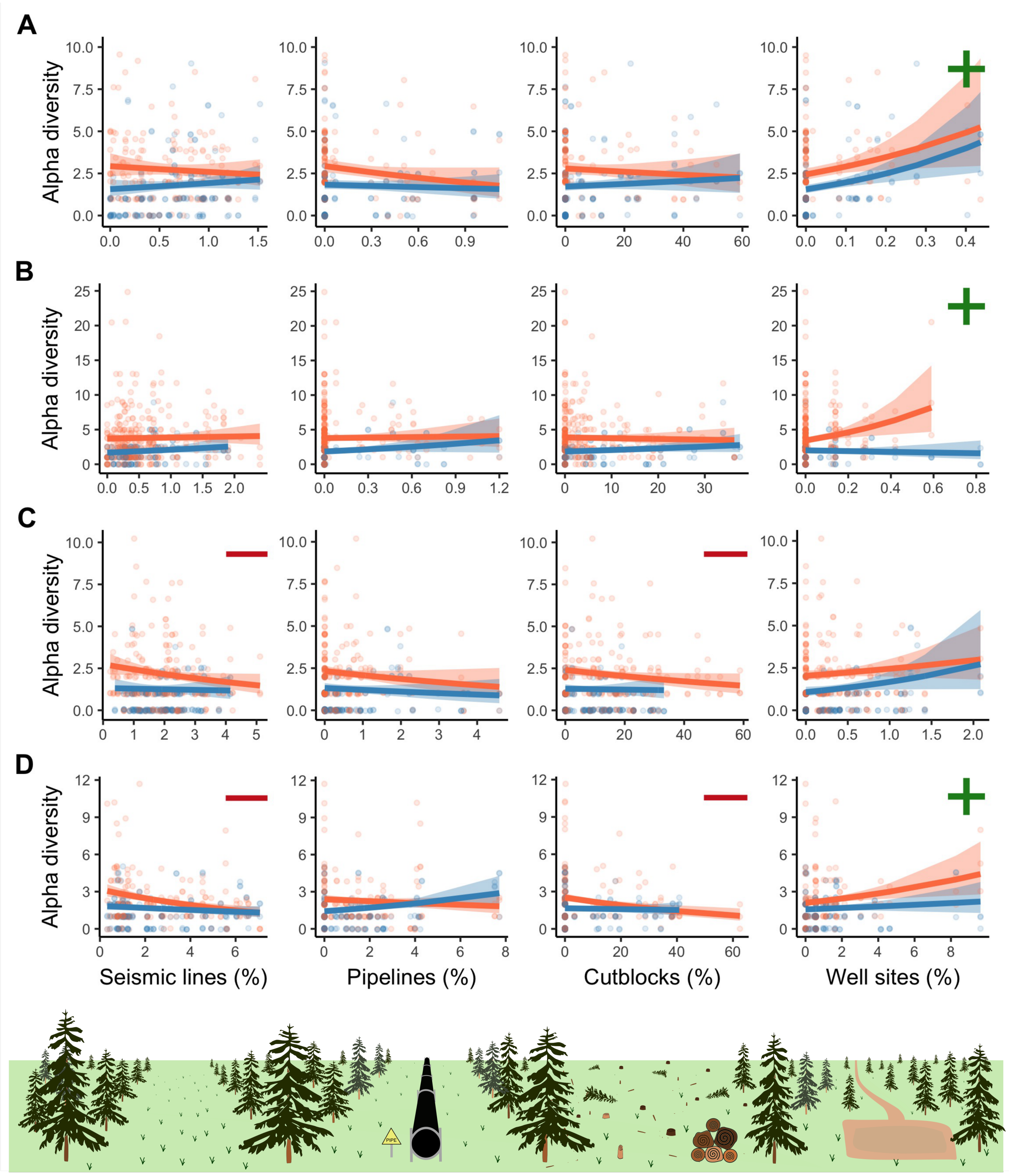

Figure 2.3. Predicted relationships between mammalian alpha diversity and the proportional coverage of anthropogenic landscape figures in four variably industrialized northwest Nearctic landscapes: HD-M1 (A), HD-M2 (B), MD-B (C), and HD-B (D). Orange and blue curves show the predicted relationship during 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.

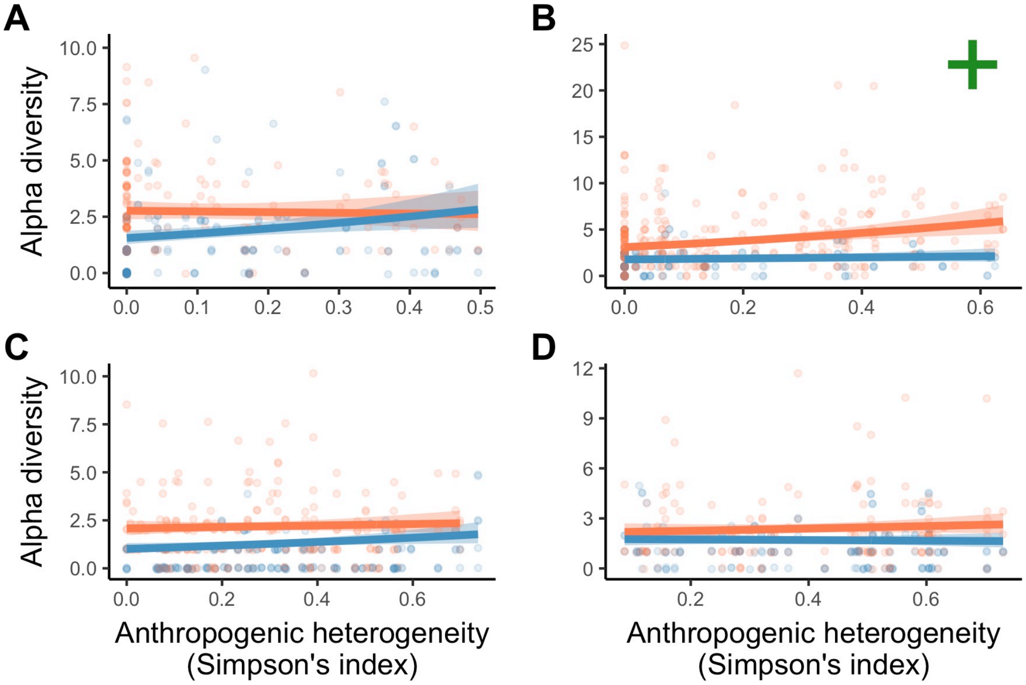

Figure 2.4. Predicted relationships between mammalian alpha diversity and anthropogenic heterogeneity, calculated using Simpson's index, in four variably industrialized northwest Nearctic landscapes: HD-M1 (A), HD-M2 (B), MD-B (C), and HD-B (D). Orange and blue curves show the predicted relationship 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.

2.4 Discussion

I 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 some hypothesized natural diversity determinants in heavily modified environments. Conversely, I 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. I also found that alpha diversity increased with the coverage of petroleum-extraction well sites in each highly industrialized landscape, revealing that well sites may be an anthropogenic keystone structure in highly industrialized landscapes. In contrast, I 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^2 well-outweighed anthropogenic diversity 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 diversity determinants at local scales compared to regional scales.

The keystone structures hypothesis has previously focused on natural keystone structures (Tews et al., 2004), but I 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, similar to 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 my 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 mammalian 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 industrialized (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 I considered only a limited set of possible diversity determinants (Atauri & De Lucio, 2001), and that I measured alpha diversity over 30 days, centering my conclusions on species' short-term space use. Additionally, I 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, my 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, my 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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Chapter 3

White-tailed deer invasions alter predator–prey associations in an industrialized boreal forest

This chapter will be submitted for publication with coauthors A. Cole Burton, Eric Higgs, and Jason T. Fisher.

3.1 Introduction

Mammalian predators play a key role in maintaining biodiversity (Estes et al., 2011). Through direct predation and indirect trophic cascades, mammalian predators facilitate species coexistence, support ecosystem functioning, and increase ecosystem stability (Crooks & Soulé, 1999; Estes et al., 2011; Wallach et al., 2015). While some mammalian predator species (e.g., apex predators) affect ecosystem dynamics more strongly than others (Estes et al., 2011), predators' collective contributions to ecosystem functioning commonly increase with predator species diversity (Brose & Hillebrand, 2016; Bruno & Cardinale, 2008). It is therefore important that we maintain entire predator communities for the conservation of biodiversity (Finke & Snyder, 2010). To effectively do so, however, we must better understand the mechanisms through which sympatric mammalian predators coexist.

Species coexistence is believed to be facilitated primarily by resource partitioning, as multiple species with identical niches cannot coexist according to the competitive exclusion principle (Amarasekare, 2003). Resource partitioning may occur by behavioural changes in species' resource use, where species adjust their realized niches to weaken interspecific competition on ecological time scales (e.g., Ritchie and Johnson, 2009), or by natural selection, where interspecific competition causes species' fundamental niches to diverge on evolutionary time scales (Schluter, 1994; Schoener, 1974). Either way, predator species may coexist by partitioning any type of divisible resource, such as habitat, time, or prey.

The possibility that large mammalian predator species coexist by partitioning prey is particularly interesting, as many mammalian predators are facultative scavengers; in addition to killing prey, many mammalian predators scavenge on carrion provided by other predator species (Pereira et al., 2014). By doing so, many mammalian predators both compete with and are facilitated by other predator species, which might alter the ecological forces promoting that sympatric predator species hunt different prey species. Although many studies have approached the topic of prey partitioning by comparing the diets of a few functionally similar mammalian predator species (Arjo et al., 2002; O'Donoghue et al., 1998), fewer studies have considered the broader community of hunters and scavengers and used information from species' distributions.

The boreal forest of North America contains a simple and well-studied mammal community that has long served as a model system for understanding predator–prey dynamics (Krebs et al., 2001), thus providing an ideal system for studying how predators partition prey. Over recent decades, however, the historical predator–prey dynamics of many boreal mammal communities have been heavily altered by anthropogenic activities (McKenzie et al., 2012; Venier et al., 2014). Firstly, linear and polygonal forest clearings have been introduced throughout densely forested habitats for natural resource extraction, allowing top predators, namely wolves (*Canis lupis*), to more efficiently and frequently encounter prey (Dickie et al., 2017; McKenzie et al., 2012). Secondly, early seral vegetation has been made ubiquitous by anthropogenic forest clearings and declining winter severity, allowing white-tailed deer (*Odocoileus virginianus*) to invade much of the southern boreal where they have established as a new, abundant prey species (Dawe & Boutin, 2016; Fisher & Burton, 2021). Resultingly, the boreal forest now provides a valuable system in which to investigate not only how predators partition prey but how an invasive prey species alters historical predator–prey interactions.

I studied mammalian predator–prey associations in an industrialized boreal forest landscape to investigate (1) whether predator species partition prey species and (2) how white-tailed deer modify predator species' associations to historically important prey species. I hypothesized that predator species do indeed partition prey, for which I predicted that each predator species would be positively associated with a unique set of prey species.

3.2 Methods

3.2.1 Study region

I used camera trap data collected from the boreal forest 140 km northeast of Lac La Biche, Alberta, Canada (Figure 3.1). This region is naturally composed of black spruce (Picea mariana), white spruce (*Picea glauca*), and aspen (*Populus tremuloides*) forests alongside peat-dominated wetlands. Due to natural resource extraction, the region is heavily fragmented by petroleum-exploration seismic lines, petroleum-extraction well sites, and forestry cutblocks, among other industrial features (Pickell et al., 2015; Venier et al., 2014). Camera traps were deployed across an industrialized area of 3000 km^2 in which natural habitats and industrial landscape features are both prominent (see Fisher and Burton, 2018).

3.2.2 Sampling design

I used data from 61 camera traps (Reconyx PC900 Hyperfire; Holmen, WI) deployed using a stratified-random sampling design. As described in Fisher and Burton (2018), camera sites were chosen by superimposing a stratified grid over the study area from which 1 km^2 cells were randomly selected. The grid was stratified by canopy cover, topography, and tree species, which were measured using the Alberta Vegetation Index (Nesby, 1997), and selected cells were spaced at least 2 km apart. Within each selected cell, one camera was placed along a game trail that had evidence of animal use, thus increasing the probability of detecting an animal given presence. Cameras were separated by an average minimum distance of 3.1 km (standard deviation = 1.2 km) to minimize spatial autocorrelation. Cameras were active from October 2011 to October 2014 and were not baited or lured.

3.2.3 Measuring species abundance and landcover

I considered five predator species: grey wolf (*Canis lupus*), black bear (*Ursus americanus*), coyote (*Canis latrans*), lynx (*Lynx canadensis*), and red fox (*Vulpes vulpes*). I also considered five prey species: white-tailed deer, moose (*Alces alces*), woodland caribou (*Rangifer tarandus caribou*), snowshoe hare (*Lepus americanus*), and red squirrel (*Sciurus vulgaris*). I chose these species because they represent a large portion of the mammal community and were detected enough times to allow for statistical analyses. I measured the relative abundance of each species, defined as the number of independent

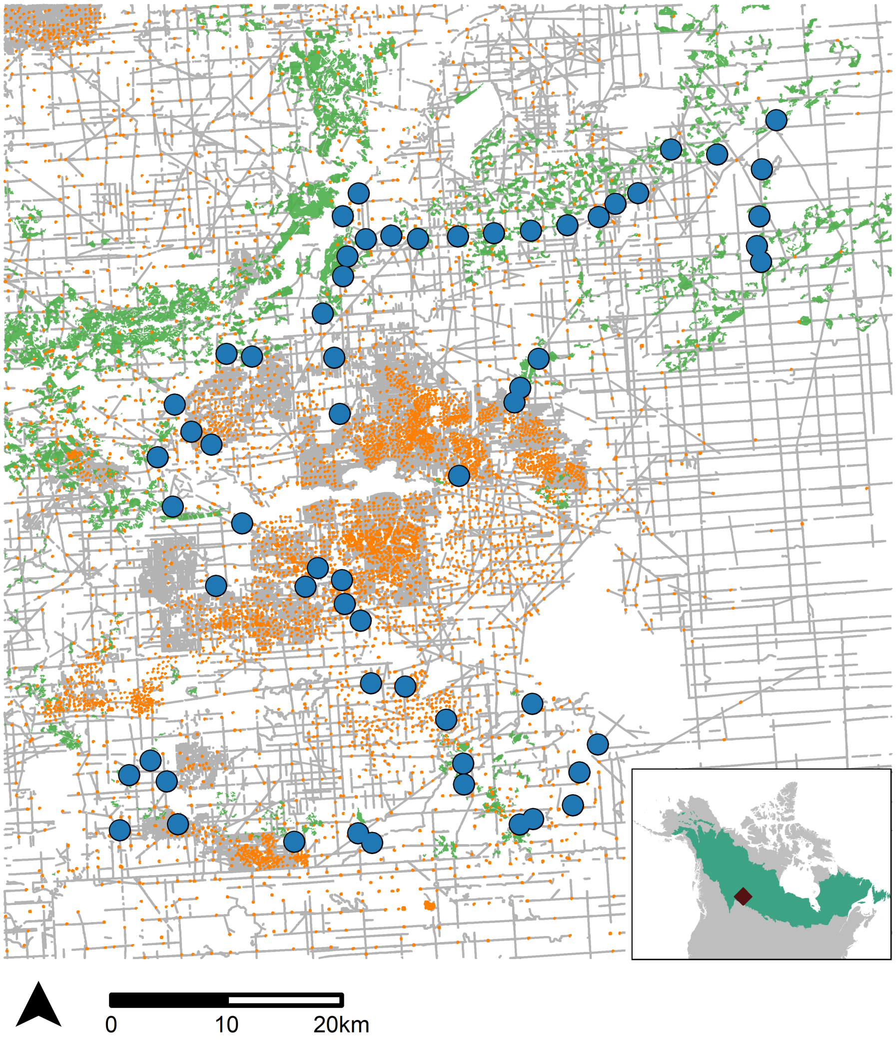

Figure 3.1. The location of 61 camera traps (blue dots) used to measure species' spatial associations in an industrialized boreal landscape. Green and orange polygons show cut-blocks and petroleum-extraction well sites, respectively, and grey lines show petroleum-extraction seismic lines. The inset plot shows the study region and the extent of the boreal biome (green) across North America.

images of each species at each camera trap, every six months during the three year sampling period. I considered images of the same species to be independent if they were taken more than 1 hour apart.

I used satellite-derived landcover datasets to measure the coverage of natural and anthropogenic landscape variables within a circular buffer around each camera site. To parsimoniously consider only the most important landscape features at their relevant spatial scales, I used the landscape features that best explained predator occurrence according to Wittische et al. (2021). Accordingly, I considered the proportional coverage (hereafter ’proportion’) of upland deciduous and lowland mixedwood within 1.75 km of each camera, as well as the proportion of anthropogenic block features (petroleum-extraction well sites and forestry cutblocks) and seismic lines within 0.5 km of each camera. I obtained these data from the Alberta Biodiversity Monitoring Institute Human Footprint Inventory (Alberta Biodiversity Monitoring Institute, 2021) from 2011.

3.2.4 Joint species distribution models

I used joint species distribution models to explain predator species’ relative abundances from prey species’ relative abundances, which I implemented using the Bayesian inference-based *Hmsc* R package (Tikhonov et al., 2020). Joint species distribution models regress a multivariate response variable (a matrix describing species’ abundances or occurrences) against a set of explanatory variables while using random effects to model the strength of associations (hereafter ’species’ residual associations’) between each species within the response variable. Species’ residual associations are estimated by the covariance of the model’s residuals and are thus estimated after controlling for variability in the fixed predictor variables (Ovaskainen & Abrego, 2020). Species’ residual associations may therefore be used to infer species interactions, albeit cautiously (Blanchet et al., 2020), when all important landscape variables are included as fixed effects in the model (Ovaskainen & Abrego, 2020).

I used the relative abundance (hereafter ’abundance’) of each predator species to form a five-dimensional response variable. In this response variable, each column was a different predator species and each row was a species’ abundance during one of six six-month periods throughout the three-year sampling duration. I assumed that cameras were operational for the entire sampling duration.

For model covariates, I included 10 fixed and one random effect. For fixed effects, I included each of the five prey species’ abundances, the proportion of upland deciduous, lowland mixedwood, anthropogenic block features, and seismic lines, and season (summer, November–April, or winter, April–November). I included the four landcover covariates to explain variation in predator species’ abundances that may otherwise be attributed to prey species’ abundances, and I included season to account for bears’ hibernation during winter and potential seasonal variability in species’ detection probabilities. I included the coordinates of each camera site as the random effect to account for the repeated six month-long measurements at each camera and to estimate predator species’ residual associations. I standardized covariates (mean = 0, standard deviation = 1) before analysis.

3.2.5 Estimating predator–prey associations

I estimated model parameters in a Bayesian framework with Markov chain Monte Carlo (MCMC). I assumed that predator species’ abundances followed a log-normal Poisson distribution, and I used the default priors of *Hmsc*. I used three MCMC chains to sample the posterior distribution, each of which was composed of 4.375 million iterations using a burn-in of 1250 and transient of 2.5 million, resulting in 1500 samples per chain. I ensured MCMC convergence by examining trace plots and the potential scale reduction factor, which was approximately 1.05. I assessed model fit using Pseudo-R^2 values, as described in Ovaskainen and Abrego (2020).

To compare the relative importance of each prey species, I calculated the proportion of explained variance that was attributable to each prey species. I did this for each predator species to then compare the importance of each prey species for each predator species. For each predator species, I also partitioned the explained variance across covariate groups, which were prey, natural habitats, anthropogenic features, season, and site. To measure the effect of each prey species' abundance on each predator species' abundance, I estimated the mean of the posterior distribution associated with each prey species. I considered effect sizes to be significant if the 95% credible interval did not overlap zero.

3.3 Results

3.3.1 Prey abundance variably explained predator abundance

Considering the combined influence of all prey species, prey abundance variably explained predator species' abundance: Black bear (pseudo-$R^2 = 0.02$), coyote (0.06), lynx (0.11), wolf (0.03), red fox (0.05) (Figure 3.2). The full model also variably explained predator species' abundance: Black bear (pseudo-$R^2 = 0.62$), coyote (0.41), wolf (0.15), lynx (0.37), red fox (0.10). The combined influence of prey abundance was comparable to the combined influence of natural and anthropogenic landcover for each predator species: Black bear (pseudo-$R^2 = 0.02$), coyote (0.06), lynx (0.09), wolf (0.05), red fox (0.06).

Different predator species' abundances were best explained by the abundance of different prey species. Partitioning the variance explained by prey across the different prey species, white-tailed deer abundance best explained the abundance of both black bear (55% of pseudo-R^2 attributable to prey abundance) and wolf (57%). Conversely,

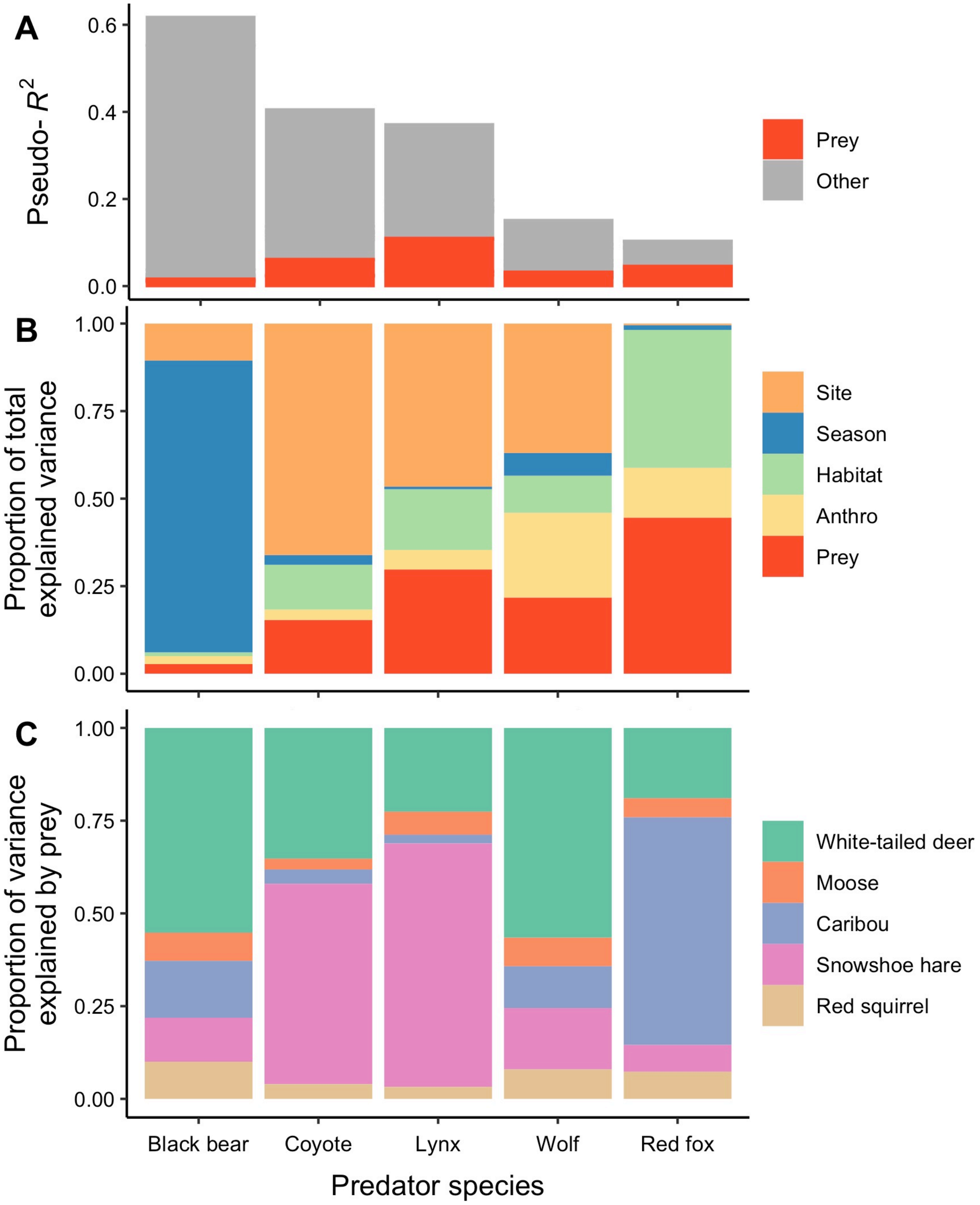

Figure 3.2. (A) Variance in predator species' abundances explained by the full model and prey species' abundances; (B) Explained variance in predator species' abundance partitioned across covariate groups; (C) Explained variance in predator species' abundance partitioned across prey species.

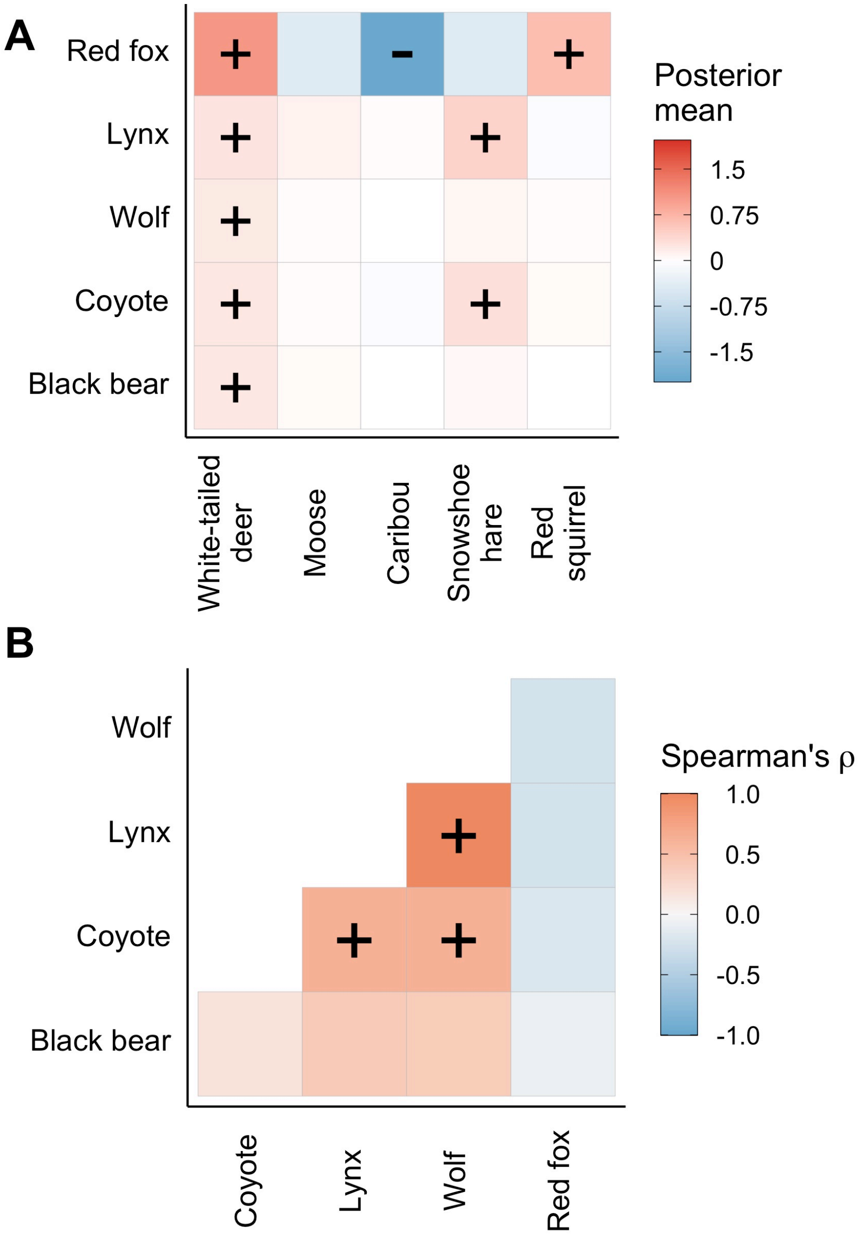

Figure 3.3. The effect sizes of prey species' abundances on predator species' abundances (A) and predator species' residual associations (A), estimated using joint species distribution models with Bayesian inference. The direction of significant effect sizes and species associations (where the 95 credible interval of the posterior mean did not overlap zero) are shown with a positive or negative sign.

snowshoe hare abundance best explained the abundance of both coyote (54% of pseudo-R^2 attributable to prey abundance) and lynx (66%), and caribou abundance best explained the abundance of red fox (61%). However, white-tailed deer abundance also explained a notable percentage of explained variance in the abundance of coyote (35% of pseudo-R^2 attributable to prey abundance), lynx (23%), and red fox (19%). Moose contributed a negligible percentage of explained variance for all predator species: Black bear (8% of pseudo-R^2 attributable to prey abundance), wolf (8%), coyote (3%), lynx (6%), red fox (5%).

3.3.2 All predators were positively associated with white-tailed deer

Predator species' abundances were variably affected by the abundance of different prey species (Figure 3.3). All predator species' abundances were positively affected by the abundance of white-tailed deer: Black bear (Posterior mean, 95% credible interval = 0.22, 0.06–0.39), wolf (0.21, 0.05–0.38), coyote (0.24, 0.09–0.39), lynx (0.26, 0.09–0.42), red fox (1.05, 0.46–1.80). None of the predator species' abundances were positively affected by the abundance of moose nor caribou. Black bear and wolf were the only predator species whose abundances were related exclusively to white-tailed deer; the abundance of coyote (0.30, 0.18–0.42) and lynx (0.44, 0.31–0.57) were also positively related to the abundance of snowshoe hare, and the abundance of red fox was also positively related to the abundance of red squirrel (0.65, 0.23–1.10).

Coyote, lynx, and wolf all had significantly positive residual associations with one another: coyote–wolf (Spearman's ρ, 95% credible interval = 0.62, 0.24–1.00), coyote–lynx (0.62, 0.26–1.00), lynx–wolf (0.99, 0.96–1.00). None of the other predator species were significantly associated, either positively or negatively.

3.4 Discussion

I found distinct variability in predator species' prey associations, where only some predators were associated with different prey species. Interestingly, all predator species were positively associated with white-tailed deer, suggesting that white-tailed deer may be consumed by the entire predator community. My findings thus provide only partial support for my hypothesis that predator species coexist by partitioning prey species. More strikingly, though, my findings suggest that the invasion of white-tailed deer into boreal ecosystems may be reconfiguring the interactions between particular predator and prey species.

Wolves, black bears, and coyotes are all known to hunt ungulates, but smaller predators are often unable to efficiently capture such large prey (Krebs et al., 2001). It is therefore possible that wolves, black bears, and coyotes were associated with white-tailed deer by directly hunting them, whereas lynx and red foxes were more likely associated with white-tailed deer by scavenging on deer carcasses (Gomo et al., 2021; Staples III, 1995). Although I cannot determine whether predators consumed their associated prey species, these findings generally align with well-established knowledge of boreal food webs (Krebs et al., 2001; Latham, Latham, Boyce, et al., 2013). It is striking, however, that none of the predator species were associated with moose, the historically important ungulate prey species in boreal ecosystems (Latham et al., 2011). This might reflect the general decline of moose populations throughout the southern boreal forest, which is notably due in part to the same anthropogenic activities that benefit white-tailed deer (Arsenault & Rodgers, 2019; Fisher & Burton, 2021). White-tailed deer may consequently be replacing moose as the primary ungulate prey species in boreal ecosystems and thus propelling major ecological change (Latham, Latham, Knopff, et al., 2013; Latham et al., 2011).

Excluding mesopredators' associations to white-tailed deer, predators generally partitioned prey by body size: wolves and black bears associated with white-tailed deer, coyotes and lynx associated with snowshoe hares, and red foxes associated with red squirrels. This reflects what is known about predator–prey mass ratios remarkably well; predators should preferentially hunt prey that are small enough to efficiently capture yet large enough to provide sufficient nutrients, causing larger predators to preferentially hunt larger prey (Brose, 2010). Interestingly, though, coyotes and lynx did not appear to partition snowshoe hares. Recalling that species with identical niches cannot coexist (Amarasekare, 2003), it is therefore likely that coyotes and lynx partition other resources, such as habitats, time, or different prey species not included in my analysis.

Apex predators have long been known to facilitate mesopredators by providing scavenging opportunities, but whether the strength of facilitation outweighs the strength of competition is unclear; apex predators may also kill, instill fear in, or directly compete for resources with mesopredators (Newsome et al., 2017; Sivy et al., 2018). My findings suggest that the strength of facilitation outweighs that of competition for some mesopredator species, as coyotes and lynx were both positively associated with wolves. Although this same pattern may arise by wolves tracking coyotes and lynx, it is more likely that coyotes and lynx tracked wolves given that coyote and lynx were also positively associated. Moreover, because these predator–predator associations were estimated after controlling for prey abundance, my findings suggest that coyote and lynx tracked wolves themselves rather than wolves' prey, likely for scavenging opportunities. In turn, if wolf declines due to human persecution (Hebblewhite, 2017) reduce carrion availability, the loss of wolves may decrease rather than increase the size of mesopredator populations, countering the mesopredator release hypothesis (Crooks & Soulé, 1999). However, it is important to emphasize that mesopredators might compensate for low carrion availability by hunting more frequently, implying that the association between coyotes, lynx, and wolves likely depends on both predator and prey densities (Pereira et al., 2014).

The Hierarchical Modelling of Species Communities framework that I used to reach my conclusions offers many advantages over alternative statistical methods. For example, as the framework can model predator–predator associations while controlling for environmental covariates, species interactions can be fairly confidently inferred (Ovaskainen & Abrego, 2020). Moreover, as the framework allows for explained variance to be partitioned across covariates, the importance of different variables can be easily and clearly compared (Ovaskainen & Abrego, 2020). However, it is important to emphasize that species' spatial associations do not necessarily imply species interactions (Blanchet et al., 2020), and that relatively important covariates may still explain only minor amounts of variation in the response variable. Nonetheless, this work will greatly inform future studies that aim to compare species' associations using camera traps.

While I reveal significant changes to boreal mammal distributions caused by the invasion of white-tailed deer, white-tailed deer are only proximate drivers of ecological change; the absolute drivers are anthropogenic landscape changes and climate change, which facilitate white-tailed deer invasions (Dawe & Boutin, 2016; Fisher & Burton, 2021). Efforts to mitigate the impacts of white-tailed deer on boreal ecosystems should therefore center on landscape restoration. In particular, the forested habitats that are characteristic of the boreal biome should be restored to reduce the availability of early seral vegetation. This would likely suppress one of the primary mechanisms that allow for white-tailed deer to expand northward and establish as a novel component of boreal ecosystems (Fisher & Burton, 2021). Without landscape restoration, however, white-tailed deer will likely continue to alter mammalian predator–prey dynamics and consequently boreal food webs.

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Chapter 4

Conclusions

4.1 Summary and synthesis

My objective was to understand both the environmental determinants of fine-scale mammal diversity and the mechanisms by which mammalian predator species coexist, building the ecological knowledge necessary to better incorporate species interactions and community dynamics into biodiversity conservation and restoration. I performed two independent but related studies to meet this objective. By doing so, I provided new information about mammal species' distributions and interactions that can help guide conservation and restoration strategies globally.

In Chapter 2, I compared natural and anthropogenic determinants of local mammal diversity. Specifically, I compared how well the proportion and heterogeneity of natural and anthropogenic landscape features, as well as productivity, explained mammalian alpha diveristy. I found that anthropogenic landscape features explained local mammal diversity better than natural features in heavily industrialized landscapes, where diversity strikingly increased with the coverage of petroleum-extraction well sites. I thus demonstrated that industrial landscape changes fundamentally alter both the patterns and processes of mammal diversity and may aggregate rather than dissipate species.

In Chapter 3, I examined whether prey partitioning facilitates the coexistence of mammalian predator species in an industrialized boreal forest landscape. I did this using joint species distribution models to simultaneously model predator–prey and predator–predator assocations. I found only partial support for my hypothesis that predator species partition prey, as some predator species were associated with the same set of prey species. Remarkably, though, I also found that each predator species was positively associated with white-tailed deer. My findings thus suggest that white-tailed deer may be replacing moose as the primary ungulate prey species in boreal ecosystems, marking a major ecological change.

These studies illustrate that industrial landscape changes alter both the distribution and interactions of mammals in the northwest Nearctic. My findings in Chapter 2 demonstrate that petroleum-extraction well sites, petroleum-exploration seismic lines, and forestry cutblocks are partly responsible for these ecological shifts. My findings in Chapter 3, however, highlight that species interactions are important proximate drivers of ecological change, at least in the boreal biome. Together, these findings illustrate that industrial landscape changes impact mammal communities through complex and diverse mechanisms composed of both direct and indirect ecological effects.

4.2 Limitations and future directions

My studies illustrate industrial landscape changes as a major driver of ecological change, but my conclusions are not without caveats and limitations. For instance, to compare the environmental determinants of mammal diversity across six different landscapes, I had to assume that variability in camera trap sampling designs had a negligible influence on species' detection probabilities. While this assumption is common in studies that synthesize camera trap data due to variability in camera trap sampling protocols (Burton et al., 2015), camera trap sampling designs likely do affect species' detection probabilities (Hofmeester et al., 2017; Kays et al., 2021). Researchers should thus establish a standardized camera trap sampling protocol and coordinate their sampling efforts (Steenweg et al., 2017) to support future data syntheses. In developing this protocol, researchers should pay particular attention to which probabilistic sampling design is used to select camera sites, as this decision will partly shape the allowable scope of ecological inference.

A major challenge in using camera traps for ecological research is linking species' spatial patterns to ecological processes (Burton et al., 2015). While I made this link most explicitly in Chapter 3 by inferring species interactions from species associations, there are many uncertainties in how well camera traps are able to capture non-spatial ecological dynamics, such as species interactions (Blanchet et al., 2020; Steenweg et al., 2017). To help resolve these uncertainties, future research should combine camera trap data with additional data types, such as behavioural and dietary data, to study species interactions through multiple lines of independent evidence. For example, researchers should directly compare species' spatial associations estimated from camera trap data to their dietary proportions estimated from stable isotope data. To directly link these data to species interactions, however, researchers must first establish how to measure the strength of species interactions, which remains a major barrier for empirical wildlife research (Kelt et al., 2019).

Ecological patterns often depend on the spatial scale at which they are measured (Levin, 1992), urging that we understand how industrial landscape changes affect mammal communities across multiple scales. Camera traps commonly survey animals at a fixed scale (i.e., a point location), centering the problem of scale in camera trap studies on the scale at which environmental explanatory variables are measured. In Chapter 2, I addressed potential scale-dependency by measuring each environmental variable over a range of spatial scales, then selecting the single best scale at which each variable explained mammal diversity. However, the optimal scale for environmental variables using this approach often depends on the variable and environmental context (Levin, 1992), causing different scales to be used in different studies. To help resolve the issue of scale and facilitate cross-study comparisons, researchers should develop a consistent set of specific spatial scales at which to explain camera trap data from environmental variables.

We have recently entered the United Nation's Decade on Restoration, which intends to prevent, halt, and reverse ecosystem degradation globally ("UN Decade on Restoration", n.d.). Ecosystem restoration across industrialized landscapes requires that we understand how industrial landscape changes alter ecosystem properties. From my findings that industrial forest clearings significantly alter mammal community dynamics, either directly or by facilitating species invasions, I recommend that restoration strategies prioritize reforestation of industrial forest clearings to help restore northwest Nearctic ecosystems. I also recommend that species interactions be considered in restoration efforts, as novel or altered species interaction may continue to propel ecological change even after natural habitats have been restored (Hobbs et al., 2009).

Camera traps are a powerful and cost-effective tools for monitoring and conserving biodiversity, which many public and private organizations around the world are now incentivized or required to do. Camera traps are thus likely to be used more frequently, and with statistical advances, become more useful, for measuring and mitigating biodiversity change. We should thus continue to develop the computational infrastructure that camera trap practictioners need to easily manage, analyze, and share camera trap data. In addition, we should streamline the process of adding camera trap data to established and accessible biodiversity databases, such as the Global Biodiversity

Information Facility. These advances would majorly benefit the global camera trapping network that is currently being developed to monitor and conserve the planet’s biodiversity (Steenweg et al., 2017).

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Appendix

Table A1. Inventory of mammal species detected by camera traps in six variably industrialized landscapes in the northwest Nearctic. Presence denoted by x.

Species	LD-M	HD-M1	HD-M2	LD-B	MD-B	HD-B
Bighorn sheep (*Ovis canadensis*)	x	x				
Black bear (*Ursus americanus*)		x	x	x	x	x
Bushy-tailed woodrat (*Neotoma cinerea*)			x			
Columbian ground squirrel (*Urocitellus columbianus*)	x		x			
Cougar (*Puma concolor*)	x	x	x			
Coyote (*Canis latrans*)	x	x	x		x	x
Deer mouse (*Peromyscus maniculatus*)					x	
Elk (*Cervus canadensis*)	x	x	x			
Fisher (*Pekania pennanti*)	x			x	x	x
Flying squirrel (*Glaucomys sabrinus*)	x		x			
Golden-mantled ground squirrel (*Callospermophilus lateralis*)	x					
Grey wolf (*Canis lupus*)	x	x	x	x	x	x
Grizzly bear (*Ursus arctos horribilis*)		x	x			
Hoary marmot (*Marmota caligata*)	x				x	
Lynx (*Lynx canadensis*)	x	x	x	x	x	x
Marten (*Martes americana*)	x	x	x	x	x	x
Mink (*Neovison vison*)	x				x	
Moose (*Alces alces*)	x	x	x	x	x	x
Mountain goat (*Oreamnos americanus*)	x					
Mule deer (*Odocoileus hemionus*)	x	x	x		x	
Porcupine (*Erethizon dorsatum*)	x					
Raccoon (*Procyon lotor*)			x			
Red fox (*Vulpes vulpes*)	x	x	x	x	x	x
Red squirrel (*Tamiasciurus hudsonicus*)	x	x	x	x	x	x
Red-tail chipmunk (*Tamias ruficaudus*)	x					
Richardson's ground squirrel (*Urocitellus richardsonii*)	x					

Table A1. Inventory of mammal species detected by camera traps in six variably industrialized landscapes in the northwest Nearctic. Presence denoted by x. *(continued)*

Species	LD-M	HD-M1	HD-M2	LD-B	MD-B	HD-B
Short-tailed weasel (*Mustela erminea*)	x					
Snowshoe hare (*Lepus americanus*)	x	x	x	x	x	x
Striped skunk (*Mephitis mephitis*)			x			
White-tailed deer (*Odocoileus virginianus*)	x	x	x	x	x	x
Wolverine (*Gulo gulo*)	x	x	x			
Woodland caribou (*Rangifer tarandus caribou*)	x			x	x	x

Table A2. The number of camera traps and independent mammal-containing images from which environmental determinants of mammalian alpha diversity were compared in each landscape (LS). Images of the same species were considered independent if they were captured more than 1 hour apart. Cams (s, w) describes the number of cameras used in summer and winter, respectively. Design describes the strategy with which camera sites were chosen, and details describes how the design was implemented. Year describes the year in which data were collected.

LS	Images	Cams (s, w)	Design	Details	Year
LD-M	14794	50, 60	Systematic, stratified random	12 x 12 km^2 grid, stratified by habitats	2009-’10, 2007-’08
HD-M1	1540	75, 58	Systematic	6 x 6 km^2 grid	2020
HD-M2	2268	109, 60	Systematic	12 x 12 km^2 grid	2014
LD-B	587	42, 45	Systematic	12 x 12 km^2 grid	2019
MD-B	1256	72, 53	Stratified random	Stratified by habitats	2019
HD-B	1393	53, 50	Stratified random	Stratified by habitats	2014