MORAINE MESOCARNIVORES PROJECT: 2017-2018 Report to Landowners and Volunteers

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EXECUTIVE SUMMARY

The *Moraine Mesocarnivores Project* (MMP) investigated the degree to which the network of protected areas, private woodlots, and developed land within the mixed-use landscape of central Alberta's heartland maintains mammalian diversity, and whether this landscape is connected to forested areas in the west and north. From 2013 through 2018 our goals were to (1) measure mammal diversity and statistically relate this to landscape structure, and (2) test for connectivity within and among protected areas by examining the movement and genetic structure of fisher (*Pekania pennanti*) populations. This work took place on Alberta's Cooking Lake Moraine, also known as the Beaver Hills Biosphere.

In November 2013 we deployed 64 sampling points in a systematic design and sampled mammal species occurrence using non-invasive genetic tagging *via* hair trapping, and camera trapping. In 2014-2015 we conducted genetic analysis on these hair samples. From November 2015 through March 2016, we repeated hair trapping and camera trapping; we also live-trapped and GPS-collared 14 fisher individuals. In 2016-2017 we (i) examined fisher genetics to understand how the forested heartland is connected to distant forested areas in the boreal forest and Rocky Mountains, and; (ii) examined how camera data of fisher occurrence represents actual fisher movement, as a guide to large-scale species monitoring. Most recently, in 2017-2018, we (iii) mapped fisher movement pathways in relation to natural and anthropogenic landcover to better understand how development facilitates (or impedes) their movement, and hence persistence; and (iv) conducted a spatial analysis of the mammalian community – from wolves to weasels – across this landscape to better understand how natural, anthropogenic, and protected area landscape features best support mammalian diversity in working landscapes.

This report represents the final analysis of this project and contains two preliminary publications that have been submitted to the journals *Conservation Biology* (point iv) and *Journal of Applied Ecology* (point iii). Previous reports outline *Moraine Mesocarnivores Project* work now published in *Biological Conservation* (point i) and *Ecosphere* (point ii). Together, the work has been presented, and won awards, at seven academic and eight public lectures at the regional, national, and international levels. It has been featured in 14 press articles varying from local to national in scope. Together, this work comprised the PhD Dissertation of Dr. Frances E.C. Stewart entitled *Understanding and sampling spatial ecological*

process for biodiversity conservation in heterogenous landscapes, and conduced at the University of Victoria (Victoria, British Columbia, Canada; 2018).

The involvement of landowners, eNGOs, and volunteers in the success of this project cannot be understated. Twenty-six of 64 wildlife camera sampling sites were situated on privately owned land. The Friends of Elk Island Society provided field technicians and volunteers to check eight camera sites on a monthly basis for two years consecutively. The Beaver Hills Initiative, Edmonton Area Land Trust, Nature Conservancy of Canada, and Ducks Unlimited were instrumental in land access, financial, and field support. The University of Alberta – Augustana Campus – and Alberta Parks provided housing, equipment, and storage. Many landowners provided a welcomed hot tea and snack while sharing their own experiences living on Alberta's Cooking Lake Moraine. In the truest sense of the word, this project has been a community collaborative involving the diversity of perspectives and strengths that Alberta's heartland has to offer.

The current component of this project has now come to a close, however we very much hope to continue this research on Alberta's Cooking Lake Moraine given future opportunity. At any point, please feel free to contact either myself (<u>fstewart@uvic.ca</u>; <u>www.StewartResearch.ca</u>), or Jason T. Fisher (<u>Jason.fisher@innotechalberta.ca</u>; <u>www.jasontfisher.ca</u>), with questions about this research. You can also keep up to date on project results and happenings by visiting the project website: www.mesocarnivore.weebly.com.

We very much appreciate your support of this research.

Best Regards,

Frances Stewart

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1.0 INTRODUCTION AND MOTIVATION

Biodiversity is declining worldwide and increasing human footprint is a primary driver (Vitousek et al. 1997, Sanderson et al. 2002, Leu et al. 2008). Alberta is a special case of this global problem. A diversity of economic opportunities - forest harvesting, agriculture, and petroleum extraction – generate a diversity of disturbance patterns in Alberta, where the rate of forest loss is one of the highest on the planet, eclipsing even the Amazonian rainforest (Global Forest Watch Canada 2014). Years of rapid development have radically changed the Alberta landscape. For example, the Alberta boreal forest is now a novel landscape, without analog historically or geographically (Pickell et al. 2013, Pickell et al. 2014, Pickell et al. 2015). The effects of wholesale habitat change on Alberta's biodiversity remain largely unknown. This is true even of "Alberta's Heartland", the mixed forest and prairie region in central Alberta.

The persistence of wildlife populations on Alberta's landscape are entirely dependent on how well that landscape functions (Wiens 1992, Wiens et al. 1993), which in turn depends on the degree of habitat fragmentation it has sustained from landscape development (Fahrig 1999, Fahrig 2001, Fahrig 2002, 2003). In central Alberta, fragmentation stems from development in multiple sectors: agriculture, petroleum extraction, rural residential properties, and transportation infrastructure. The cumulative effects of these impacts on biodiversity in the region remain, surprisingly, largely unknown. Alberta's Land Use Framework (LUF) assumes that a mix of protected areas (PAs) and remaining habitats within the "working landscape" will together support wildlife populations. This pivotal assumption in the LUF remains untested, and we know nothing about the thresholds of human impact that will permit, or prevent, wildlife populations from remaining on the landscape.

The Moraine Mesocarnivores Project tests new ideas about the biodiversity, connectivity, and conservation value of small protected areas in a landscape with cumulative effects of multiple impacts. We examinine the diversity and distribution of mammal species within a matrix of PAs and private land in central Alberta, with natural habitats contiguous with areas of significant anthropogenic disturbance. We use a combination of field, laboratory, and statistical methods to understand the diversity on the PAs, their value relative to the surrounding "working" landscape, and the connectivity between protected areas, which is so vital to maintaining persistent wildlife populations.

2.0 ACKNOWLEDGEMENTS

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3.0 FISHER MOVEMENTS DEMONSTRATE LANDSCAPE CONNECTIVITY IN ALBERTA'S HEARTLAND; AN ADVANCED APPLICATION OF BIOLOGGING

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3.1 PREFACE

This section is based on a paper conducted under the *Moraine Mesocarnivores Project*. One of the primary goals of the MMP is to scientifically investigate whether the primary assumptions of Alberta's Land Use Framework holds true: the Green (forested) Zones, and protected areas, of Alberta are functionally connected to one another although the land between them is highly developed for agriculture and other sectors. We had the unique opportunity to test this assumption by examining the refined GPS movement patterns of the fisher (*Pekania pennanti*) population on Alberta's Cooking Lake Moraine. Compared to this species' body size, individuals display a high amount of movement, making them fantastic research subjects for questions regarding landscape connectivity. This research was a collaborative effort; this paper is in preparation for submission to the *Journal of Animal Ecology* Special Issue on Biologging.

3.2 ABSTRACT

Biologging, and the simultaneous advancement of statistical methods, allows animal ecologists to sharpen their understanding of ecological processes through the use of natural experimental systems. Animal movement between resource patches is a behvioural expression of multiple ecological processes that affect individual fitness. Understanding the causes and consequences of movement variations in heterogeneous landscapes is therefore imperative to both theory development and conservation application. Protected area (PA) networks are a conservation tool used to preserve habitat patches in heterogeneous environments. The development of PA networks relies on our accurate understanding of animal movement and connectivity theory, but this understanding is rarely tested in real-world

situations due to the expanse of most PA networks. Using a tractable PA network mesocosm, we employ >19,000 fisher (*Pekania pennanti*) GPS fixes as an application of cutting-edge biologging technology to test our conceptual understanding of animal movement ecology. We analyze these data with the recently developed integrated step selection analysis (iSSA; Avgar et al 2016) to test hypotheses representing three analysis frameworks of functional connectivity (corridors, least cost paths, or stepping stones) in heterogeneous environments. Consistently, iSSA models demonstrate individuals moved along structurally self-similar corridors, rather than across heterogeneous least cost paths or between isolated islands of stepping stone habitat. Importantly, natural features within and between protected areas had the largest effect on connectivity, outweighing protected areas themselves by 6-fold. We demonstrate that natural habitat within working landscapes predicts functional connectivity better than protected areas. These results highlight the importance of a landscape matrix effect in maintaining functional connectivity across a protected area network. Importantly, they underscore our need to better understand individual animal responses to heterogeneous environments rather than relying on effective application of conservation tools from previously derived animal movement theory.

3.3 INTRODUCTION

Refined observations of individual movement patterns contribute to our understanding of animal responses to changing environments. The use of biologging devices, such as high-fix rate Global Positioning System (GPS) units, enhances the spatial and temporal resolution of animal movement relative to heterogeneity in their environment, including how animals select, and move between, partially or wholly disjunct resource patches to meet their energetic and life-history requirements. Movement is a behavioural expression of multiple ecological processes, the primary of which is resource selection within heterogeneous environments (Hooten et al. 2017): it therefore needs to be fully understood to implement effective biodiversity conservation tools as landscapes continue to change rapidly (Allen and Singh 2016; Meijer et al. 2018).

Increasing landscape heterogeneity through land use change – reduction and spatial fragmentation of already discontinuously distributed resources – is a global problem that affects individual animal movements, populations, and ultimately biodiversity persistence (Fahrig 2003; da Silveira et al. 2016; Ng et al. 2017; Sadler 2017). Animals must be able to move between areas to ensure landscape scale functional connectivity of populations (Rudnik et al. 2012). For example, through detailed and collaborative global monitoring of animal movements (i.e. Movebank.org,

ICARUSinitiative.org), decreased movement in areas of high fragmentation has been observed across multiple taxa (Tucker et al. 2018). This may be in part due to increasing proportion of landscape matrix – areas of higher risk and fewer resources that animals may or may not decide to cross in order to get to the next resource patch (Turner et al. 2001) – within landscapes of high fragmentation. The increasing abundance of these "working landscapes" – areas of high fragmentation and interspersed natural and anthropogenic features (similar to "mixed-use", "human-dominated", or "cultural" landscapes; Tscharntke et al. 2012; World Heritage Committee 2012) – is the direct result of land use change. Despite the increasing abundance of these systems we know very little about how theoretical derivations of animal movement play out as real time functional connectivity estimates, highlighting our limited understanding of (1) how animals respond to their changing environment and; (2) ultimately, how these relatively novel, and increasingly prevelant, ecosystems work.

Functional connectivity is a measure of how animals connect resources (Forman 1995). These measures are guntified under different analysis frameworks based on non-mutually exclusive theories. Based on metapopulation theory, and developed in working-landscape systems (Taylor et al. 1993; Bennett et al. 1994; Beier and Noss 1998), the corridor framework suggests that structurally similar and continuously connected habitats (ie. resource patches) surrounded by a landscape matrix will best facilitate functional connectivity between populations (Beier & Noss 1998; but see Haddad et al. 2000). Alternatively, derived from electrical circuit theory (McRae, Dickson, Keitt, & Shah, 2008), the least-cost paths (LCP) framework defines habitat by the 'cost' or 'effective distance' it imparts on animal movement. It views the landscape as a continuum of costs that correlate to the type, and density, of habitat features (Adriaensen et al. 2003); it does not consider habitat and matrix as binary, separate, entities. Finally, the Stepping Stone framework, derived from Island Biogeography theory (MacArthur & Wilson 1967), is a subset of LCP that implies physically close, and large, patches of the same habitat type (ie. resource patches) will best facilitate connectivity (Gilpin 1980); it acutely distinguishes between landscape matrix and habitat. Relative support for each connectivity analysis framework can be inferred from measuring the pattern, rate, and direction of animal movement and habitat selection between patches and across a tractable landscape (Tischendorf & Fahrig 200a;200b; Goodwin 2003).

Protected areas (PAs) are a conservation tool that protect resource patches with the goal of increasing species persistence. The IUCN's Convention on Biological Diversity Aichi Target 11's (CBD 2020) requiring 17% of the globe's terrestrial area to be designated as protected is rapidly approaching.

However, these protected areas need to be functionally connected into protected area networks (PANs; IUCN 2018); that is, the landscape matrix between PAs must be able to support animal movements to ensure efficacy of biodiversity conservation within PAs. Without advanced measurement tools such as biologging, paired with refined statistical models, to test our theoretical understandings of animal movement, we may not be able to predict functional connectivity in these conservation contexts. However, by using a landscape mesocosm (Odum, 1984) – an area of representative global land use change that provides a link between empirical (e.g. Clark et al. 2015), modeling (e.g. Royle et al. 2013, Morin et al. 2017), and simulation studies (e.g. Fahrig 1991; Epperson et al. 2010) – and collecting a high density of biologging data from a model species simultaneously representative of generalized animal movements and biodiversity, we can test ecological concepts of functional connectivity spanning the entire landscape.

To better understand animal resource acquisition in a globally relevant context, we combine leading edge biologging with the recently developed iSSA statistical method (Avgar, Potts, Lewis, & Boyce, 2016), to analyze animal movement and habitat selection within a tractable landscape mesocosm. To our knowledge, we employ the most extensive, and high resolution, GPS telemetry data yet collected from fisher (*Pekania pennanti*), a species subject to extensive connectivity and biologging research (Garroway et al. 2011, LaPoint et al. 2013, Koen et al. 2013), and is representative of general mammal biodiversity across this landscape mesocosm (Stewart et al., in review). We use biologging to compare the adherence of observed mammalian functional connectivity, measured as detailed GPS movements, to three conceptual frameworks about how landscape structure works to provide functional connectivity in heterogeneous environments.

Currently, functional connectivity theory assumes that animal movements are facilitated by the presence of discrete resource patches, such as protected areas (PAs), and can be predicted by one of three connectivity frameworks; corridors, least cost paths, or stepping stones. We sought to explicitly quantify the contribution of PAs to functional connectivity of a PA network, and evaluate how the inference of animal movements between resource patches may change if PAs within heterogeneous working landscapes are not a driver of network connectivity. Through testing our theoretical concepts of functional connectivity with refined animal movement data and advanced statistical analyses, we will be better able to understand, and predict, how animals relate to their environment in the face of rapid landscape change.

3.4 METHODS

The Beaver Hills Biosphere (BHB) covers approximately 1,596 km² of glacial moraine in east-central Alberta, Canada (53.381167°N, 113.062976°W; Figure 3.1). This heterogeneous landscape is composed primarily of native aspen parkland (*Populus tremuloides* and *P. balsamifera*), and interspersed small waterbodies, meadows, and patches of white spruce (*Picea glauca*). Seven hundred and sixty-three protected areas of varying size (mean = 784.1 \pm 290 km²), status (from local conservation easements managed by non-government organizations to provincial and national parks), and isolation (0.95 \pm 0.004 km) conserve these native features across the BHB, but are surrounded by extensive resource extraction in the form of oil and gas, agriculture, forestry, and rural-residential development. The resulting matrix surrounding the BHB's protected areas is a mosaic of private lands, roads, and agriculture that separate the BHB from tracts of contiguous forest in other parts of the province.

From November 2015 through February 2016 we used covered cage traps (Tomahawk 109, Tomahawk, WI) to live-capture 10 fisher (sensu Stewart et al. 2018). We used a combination of ketamine (concentration = 100mg/ml, dose = 12 mg/kg) and midazolam (concentration = 5mg/ml, dose = 0.3 mg/kg) to sedate individuals; we monitored vital rates and fitted individuals with GPS tracking collars (E-obs Collar 1A; Grünwald, Germany). Collars contained a GPS microchip, ultra-high frequency transmitter for telemetry and data download, and tri-axial accelerometer; the GPS was programmed to take a GPS-fix every 5 minutes if the individual was moving greater than 10 cm/s. Spatial capture-recapture (Royle et al. 2013) modeling of these data estimate the BHB fisher population to be at most 58 individuals (3.91 fishers/100 km⁻²; Burgar et al. 2018). We therefore obtained GPS telemetry data from at least 17% of the contemporary population. All research was approved by the InnoTech Alberta Animal Care Committee (2070M-A02/048/15-P01) under the Canadian Council on Animal Care.

3.4.1 Integrated Step Selection Analysis

Functional connectivity can be measured as movement of animals in relation to landscape structure (Benz et al. 2016). Step lengths, which are defined as straight-line distances between successive GPS-fixes, directly measure animal velocity (i.e. m/5min) and can be used as an estimate of animal residency time within habitat features, with shorter steps indicating longer residency time (Turchin 1998; Thurfjell

et al. 2014). Using the *movement.ssf* function in GME (www.spatialeclogy.com/gme/), available fisher step lengths were sampled from a log normal distribution parameterized on used step lengths for each individual (distribution shape varied between 3.31 - 4.45, distribution scale varied between 1.99 - 1.40). Step lengths were ln-transformed (sensu Prokopenko et al. 2016; ln*StepLength*) to decrease the tail length of this distribution. Available turn angles were sampled from a uniform distribution between $-\pi$ and π radians (sensu Avgar et al. 2016) and are defined as the angular deviation between two headings; these values were cosine-transformed (cos*TurnAngle*), which transitions a circular measure (radians) into a linear measure between -1 and 1 (Barraquand & Benhamou, 2008; Prokopenko et al., 2016); values approaching 1 represent linear movement (Benhamou 2004). Therefore, steps without a proceeding step (i.e. the first step collected for each individual) were removed from the analysis.

For each used GPS-fix, 10 random available steps and turn angles were generated, and compared in a used-available, or "case-control", design (sensu Fortin et al. 2005; Figure 3.1). These observed steps and turn angles were assigned a "1", whereas available (i.e. generated in GME) steps and turn angles a "0" and together represent the binomial response variable in our conditional logistic regressions (Avgar et al. 2016). We conducted an analysis examining habitat selection and movement for each of 10 individuals to quantify support for each connectivity framework across the heterogeneous landscape mesocosm: the Beaver Hills Biosphere.

3.4.2 Landscape features as model covariates

To test the effect of landscape features on step length, we used ArcGIS v10.3 (ESRI, Redlands, CA, USA) Geographic Information System to quantify landscape heterogeneity. We used the LandSat digital map inventory from the Beaver Hills Biosphere (Land Management Framework 2015) to quantify the distance of the end points of fisher steps (m) to each landscape feature, as well as the density of landscape features, across 15 categories representing natural, anthropogenic, and PAs; bare landscape, crops, deciduous forests, mixed forests, coniferous forests, wetlands, development, forage, grasslands, lakes, shrubs, protected areas, rail lines, roads, streams, and protected areas (Table 3.1). Landscape feature density was calculated as the raster density of a buffer around the end point of each step, where the buffer radius was determined by the mean fisher step length (106 m; i.e. # of raster pixels/m²). We scaled these measures to allow comparison of coefficients within regression models as a measure of explained variance; these scaled distance, and density, measures comprise the predictor variables in our conditional logistic regressions.

Our final data set comprised 214,148 used and available steps across 10 fisher individuals, including (1) used/available status, step length, turn angle, fisher ID, UTM coordinates, and strata of available steps; and (2) the relationship of each step to landscape predictor variables – either the distance to, or density, of 15 landscape features (Table 3.1).

3.4.3 Statistical analyses

We created statistical models to test three non-mutually exclusive hypotheses of landscape connectivity derived from current analysis methods: corridors, least cost paths, or stepping stones (Table 3.2). We developed a 'core model' of assumed habitat features explaining variation of fisher movement in a homogenous landscape and included this model within each of our connectivity hypotheses (Table 3.2). In*StepLength* (m) represents the linear displacement between consecutive steps – a proxy for animal velocity as the time between steps is constant (m/5-minutes) – whereas the movement directionality, or tortuosity, is described by the cosine of the turning angle (Turchin 1998; Avgar et al. 2013). Including In*StepLength* and cos*TurnAngle* as model predictors within a clogit regression extends the step selection function framework (Fortin et al. 2005; Thurfjell et al. 2014) into an integrated Step Selection Analysis (iSSA), accounting for animal movement velocity and directionality within selected habitat features (Avgar et al. 2016).

From previous research we expect tortuosity and velocity to affect fisher movement and fisher to select areas of deciduous forest, coniferous forest, and mixed forest, while remaining proximate to water bodies (Aubry et al., 2013; E. Koen, Bowman, Findlay, & Zheng, 2007; LaPoint et al., 2013; Weir, 2010). These are what we define as 'low' resistance habitats for fisher. We therefore included the cos*TurnAngle*, In*StepLength*, distance to wetlands, deciduous, coniferous, and mixed forests, as well as density of deciduous, coniferous, and mixed forests within our core model. If fisher movement and habitat selection on the BHB corresponds to a corridor framework of functional connectivity, then we predict fishers should move along structurally self-similar corridors; each fisher step, as well as the previous step, will remain close to features that are linear (streams, rail lines, roads), and within features that are polygonal (wetlands, crops, forest, etc.) – whether natural or anthropogenic (Table 3.1). We therefore included the distance of each step to linear features, the distance of the previous step to

linear features, the density of habitat features around each step, the density of habitat features around the previous step, as well as core model covariates as predictors within our corridor model (Table 3.2). Alternatively, if fisher display a least cost paths (LCP) pattern of movement and habitat selection, then we predict fisher to display tortuous and short step lengths within habitats of low resistance, and linear but long movements within habitats with high resistance; on top of our core model predictors, we included an interaction between habitat density and both the cos*TurnAngle* and ln*StepLength* as predictors within our LCP model. Finally, if fisher display a stepping stone pattern to movement and habitat selection, then we expect fisher to use discrete areas of protection and have a high residency time within these areas. They should display highly tortuous movements and short step lengths within these habitats; in addition to core model predictors, we included protected area presence (0/1) and interactions between protected area presence and both cos*TurnAngle* and ln*StepLength* within our stepping stone model.

We competed each of the three models (corridor model, LCP model, and stepping stone model) in an Information Theoretic approach using Akaike Information Criterion values (AIC; Burnham and Anderson 2002; Table 3.2). We used the *clogit* function in the *Survival* package (Therneau 2015) in R (v3.2.2 R Foundation for Statistical Computing), to perform a total of 50 conditional logistic regressions (50 models – 5 for each individual: three hypothesis models, a core model and a global model; Table 3.2). The response variable was steps observed (0/1), and each strata was assigned to paired used:available steps (*sensu* Prokopenko et al. 2016). We performed a variance inflation analysis to remove predictor collinearity, and thoroughly explored our data (*sensu* Zuur et al. 2009) ensuring all *clogit* model assumptions were met. All statistical analyses were conducted in R (R Foundation for Statistical Computing), and results are presented as mean ± SE unless otherwise specified.

3.5 RESULTS

Of the 14 fisher captured and collared, we obtained GPS data from 10 individuals (5 males: 5 females); the 4 other collars either did not collect data, or were too damaged after deployment to be retrieved. These 10 collars collected 19,578 GPS fixes, over an average of 32.97 days (minimum = 4.87 days, maximum = 90.79 days) of continuous movement data per individual. Fisher step lengths over a 5-min fix interval approximated a gamma distribution with many small steps (105.47 m \pm 1.85 m, min = 0.06 m, max = 2972.0 m), and turn angles were on average positive, indicating significant directional movement behaviour (0.08 rad \pm 0.0001 rad). The corridor model of functional connectivity received the highest AIC weight of evidence across 6 of the 10 fisher individuals (86-99%), and second highest support for the remaining 4 individuals. No individuals showed support for either the least cost paths or stepping stone hypothesis (Figure 3.2). Among fisher individuals, natural and anthropogenic features best explained the observed variance in fisher steps; PA predictors (density, distance to, and interactions with either In*StepLength* or cos*TurnAngle*) were rarely significant in top models. Only two of 10 top-individual models contained significant PA predictors; one fisher individual's movement and habitat selection significantly varied with PA density of the current ($\beta = 0.20 \pm 0.04$, p < 0.001) and previous ($\beta = 0.15 \pm 0.04$, p < 0.001) step, which supported our stepping stone predictions. The second fishers' movement and habitat selection also varied positively with PA density of the previous step ($\beta = 0.89 \pm 0.41$, p = 0.04), but not of the current step: generally this animal was leaving a PA. Of the other eight individual fishers, three individuals had PA predictors in their top models, but these parameters were never significant. Selection for the presence, and specific features, of protected areas differed between fishers. Instead, fisher always selected for at least one type of natural feature.

Natural features within top models explained the majority of observed variance in individual movement patterns. Across individual models, PA parameters explained 0 to 24.1% ($11.1\% \pm 1.1\%$) of the observed variance, while natural features explained 26.1 to 99% ($73.0 \pm 7.2\%$), and anthropogenic features explained 0 to 49.7% ($24.6 \pm 7.3\%$). Among all three models competed for each individual (corridor, LCP, and stepping stone), natural features accounted for the majority of the observed variation in fisher movement and habitat selection across the heterogeneous working landscape of Alberta's Beaver Hills Biosphere (Figure 3.3).

3.6 DISCUSSION

Natural habitat within working landscapes predicts functional connectivity better than protected areas. Fishers moved along structurally self-similar corridors, rather than across heterogeneous least cost paths or between isolated islands of stepping stone habitat; fishers remain close to, and within, consistent habitat features from one step to the next. By examining functional connectivity patterns both within and between protected areas (PAs) comprising a tractable mesocosm PA network these results extend studies demonstrating an effect of the landscape matrix on PA efficacy (Baum et al. 2004; Prevedello et al. 2010; Leroux & Kerr 2013; Boesing et al. 2017) to (1) highlight the importance of the landscape matrix in maintaining functional connectivity across a PA network, and (2) increase our understanding of animal responses to both resource, and matrix, patches within heterogeneous environments.

There is substantial monetary and political capital investment in PA protection (Watson 2014). However, the investment typically ends at the PA border, and mechanics of biodiversity conservation in the matrix is left purely to hope. Here, we show that conservation tools cannot rely on either proximity or hope – we need to better understand animal responses to environmental heterogeneity, and we need a planned and protected matrix designed from correct theoretical underpinnings to provide effective biodiversity conservation across PA networks.

3.6.1 Challenging our conceptual understanding

The theory of Island Biogeography (MacArthur & Wilson 1967) first provided the conceptual framework that functional connectivity of discrete habitat patches depends on their size and isolation from other suitable patches. In this framework, the space between habitat patches – the landscape matrix (Turner et al. 2001) – is important, but purely inhospitable. This is true of oceanic islands, but in terrestrial studies the matrix provides a continuum of suitability (Dunning et al. 1992; Karieva and Wennergen 1995) that can render nearby habitat patches as effectively isolated (Ricketts 2001). The matrix can provide varying degrees of facilitation, or impediment, for functional connectivity (Baum et al. 2004; Saura et al 2018), species richness in remnant forest patches (Gascon et al. 1999), or protected area efficacy (Leroux & Kerr 2013).

It is now clear that the matrix is only as valuable as the remaining habitat patches within a landscape: if suitable habitat loss is above 80%, matrix quality no longer buffers extinction thresholds (Boesing et al. 2018). Andren (1994) demonstrated a similar finding across birds and mammals; he attributes this finding to the fact that above 70% of habitat loss, percolation theory predicts an additive effect of habitat loss and fragmentation. Corridors, which are habitat, are meant to overcome this "percolation effect" by forcing connections between habitat patches and thus preventing the additive effect with habitat fragmentation. Here, in our empirical test of these concepts, prioritizing forest features between PAs best facilitates corridor functional connectivity within PA networks for fishers and other forest-dependent species that comprise the bulk of biodiversity on this forested landscape.

If PAs conserve prime habitat patches, we predicted fisher movement to display highly tortuous and short steps as an indication of high residency time within these areas. However, we found variable support for this concept within individual movements: 40% of fisher displayed linear and long steps, 20% of fisher displayed linear and short steps, 20% of fisher displayed tortuous and short steps, and 20% of fisher had no variation in their steps as they only occurred in protected areas. Therefore, 40% of the data support our prediction, and 60% of the data do not. Across individual movements within PAs, step length (r = 0.003, df = 214150, p = 0.11) and turning angles (r < 0.001, df = 214150, p = 0.82) were not significantly associated with conifer density. Individuals displayed longer step lengths in PAs with dense mixedwood forests (r = 0.03, df = 214150, p < 0.001), but had no relationship with turning angle in these areas (r = < -0.001, df = 214150, p = 0.85). However, within deciduous portions of PAs, individuals displayed significantly shorter (r = -0.12, df = 214150, p < 0.001) but linear steps (r = 0.004, df = 214150, p = .0.2). These results, which only partially support our predictions, highlight four important points: (1) PAs may not be conserving prime habitat patches within this system, (2) our lack of predictability of animal responses to supposedly desirable, and therefore protected, habitats within heterogeneous environments, (3) the importance of understanding individual variation and plasticity in behavioural responses to resource acquisition under environmental variation (Dingemanse et al. 2010), and (4) the importance of considering matrix effects on predicted movement and behavioural variations within protected areas.

3.6.2 Biologging as an application to increase our understanding of animal responses to environmental heterogeneity

Animal-defined corridors are an important consideration for connectivity, as animal responses to environmental heterogenetiy demonstrate individual variation (Ramette et al. 2007) and potential for plasticity (DeWitt & Schneider 2004; Colbert et al. 2009). In a similar study to ours, where the landscape matrix had a greater proportion of urban landscape, LaPoint et al. (2013) demonstrate fisher movement data at local scales best supports a corridor model of functional connectivity, but more importantly, that fisher-defined corridors are composed of a variety of land cover types. We build upon these results to show individual variation between functional connectivity frameworks, as 4 of 10 fisher iSSA models best supported a global model rather than a model representing any specific hypothesis. This result may highlight plasticity in individual responses to environmental heterogeneity, an individual's ability to use multiple connectivity frameworks to piece together resources, or an inability to completely quantify the movement inference space within the BHB mesocosm. We demonstrate that PA network functional connectivity can be improved by incorporating individual behavioural data, rather than assuming a uniform response by individuals to structural connectivity. These 'animal-defined' corridors quantified in heterogeneous landscapes (Vogt et al. 2009) will help to parameterize the functional components of connectivity across seasons, and both natural (*e.g.* forest fires) and anthropogenic (*e.g.* crop rotation, development) disturbances (*sensu* LaPoint et al. 2013; Panzacchi et al. 2016; Abrahms et al. 2017).

The current state of biologging science allows for data collection that challenges our understanding of connectivity conservation. Combining these high-resolution data (e.g. GPS telemetry on Movebank.org), with detailed GIS data within an iSSA framework, allows for near real time integration of connectivity concepts across landscapes of varying heterogeneity. Our PA network mesocosm analysis suggests limited value of PAs in maintaining landscape connectivity unless consideration of natural features within the matrix receives protection equal to the patches they connect. In addition to creating new protected areas under the Aichi Target 11 (CBD 2020), focusing on maintaining or restoring natural landscape features within the matrix of existing PA networks, or creating PA networks within existing landscapes of high natural features, will greatly aid conservation objectives. Using biologging, these objectives can now be regularly monitored and adapted as necessary within an adaptive management framework (Walters 1986), elucidating important patterns that challenge our conceptual understanding of animal ecology and conservation science. Through employing this biologging approach, we show that increasing the extent of the global protected area network is not a stand-alone solution to connecting protected areas; the conservation of natural landscape features between PAs is the mortar that binds them together.

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3.8 TABLES AND FIGURES

Table 3.1. Distance to (*Dist*), and density around (*Dens*), the end of both used and available fisher steps were quantified across 15 landscape features within the Beaver Hills Biosphere.

Category	Landscape feature	Feature type	Description
Natural features	Bare	Polygonal	Distance to, and density, of exposed land
	Deciduous forests	Polygonal	Distance to, and density, of deciduous forest; native natural forest stands of primarily aspen or balsam poplar
	Coniferous forests	Polygonal	Distance to, and density, of coniferous forest; native natural forest stands of primarily white or black spruce
	Mixed forests	Polygonal	Distance to, and density, of mixed forests; native natural forest stands of mixed deciduous and coniferous species
	Wetlands	Polygonal	Distance to, and density, of water bodies; wetlands and ephemeral lakes
	Grasslands	Polygonal	Distance to, and density, of grassland; native natural grass cover
	Lakes	Polygonal	Distance to, and density, of water bodies; lakes
	Shrubs	Polygonal	Distance to, and density, of shrub-land; native natural
	Streams	Linear	shrub cover Distance to, and density, of water bodies; streams and
Anthropogenic features	Development	Polygonal	small rivers Distance to, and density, of built-up land (e.g. residential, municipal, or commercial)
	Crops	Polygonal	Distance to, and density, of annual and perennial crops
	Forage	Polygonal	Distance to, and density, of pastures and forages
	Rail lines	Linear	Distance to, and density, of rail transport lines
	Roads	Linear	Distance to, and density, of hard roads, vegetated roads, and trails
Protected areas	Protected areas	Polygonal	Distance to, and density, of parks and protected areas; protected area of any status (e.g. public lands, provincial parks, provincial recreation areas, national parks, conservation areas, and NGO sites

Table 3.2. Parameters within each *clogit* model describing hypothesized frameworks for landscape

 connectivity across the Beaver Hills Biosphere.

Hypothesis	Model Covariates
Corridors	Core model +
	Dist(each linear features) +
	Dens(each habitat feature) +
	<i>Dist</i> _u (each linear features) +
	Dens. (each habitat feature)
Least Cost Paths	Core model +
	Dens(all habitat features):cosTurnAngle +
	Dens(all habitat features):lnStepLength
Protected Area Stepping	Core model +
Stones	Protected area presence/absence +
	Protected area presence/absence:cos <i>TurnAngle</i> +
	Protected area presence/absence:ln <i>StepLength</i>

*All models involved a set of Core model variables that we hypothesized would be generally important to fisher movement: CosTurnAngle + InStepLength + Dist(DECID) + Dens(DECID) + Dist(CONIF) + Dens(CONIF) + Dist(MIXED) + Dens(MIXED) + Dist(WATER)

** Distance to (Dist) and density around (Dens),

: denotes an interaction



Fig. 3.1. Fisher GPS telemetry locations were collected across the protected area network of the Beaver Hills Biosphere in east-central Alberta, Canada. For each used GPS step, 10 random available steps and turn angles were generated. These points were compared in a used-available, or "case-control", design to determine the density and configuration of habitat features predicting used points.



Fig 3.2. High fix-rate GPS movement telemetry data from six of 10 fisher individuals showed the highest relative support for a corridor framework of functional when compared to either least cost paths or stepping stone framework hypotheses across the heterogeneous landscape mesocosm of Alberta's Beaver Hills Biosphere.



Fig 3.3. Natural features best explained observe variation in high fix-rate GPS telemetry movement data from 10 individual fishers across the heterogeneous landscape mesocosm of Alberta's Beaver Hills Biosphere. Despite predictions, protected areas explained less than 24% of any individual's observed variation in movement.

4.0 MAMMALIAN BIODIVERSITY IN CENTRAL ALBERTA'S HEARTLAND; FROM WOLVES TO WEASELS

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4.1 PREFACE

Management decisions that effectively maintain biodiversity require information on how species relate to their environment. Scientists gather this information in multiple ways (Scott et al. 2002, Williams et al. 2002). One rapidly expanding mode of gathering species data across large landscapes is through camera trapping (Burton et al. 2015, Steenweg et al. 2016). Many Albertan agencies (government, industry, NGOs, academia) have invested heavily in camera trapping over the last decade, and it promises to be a major platform for research in the future. Though an effective species sampling tool, scientists are still working to understand how camera traps sample populations, what these data mean, and how the information can be used. In this research, we used camera data from 15 mammal species to better understand what camera data represent for mammal species' use of the landscape, and how we can use this knowledge to better inform future biodiversity monitoring and protected area designation. This chapter is from a manuscript that has been submitted to the journal *Conservation Biology* in May 2018.

4.2 ABSTRACT

Protected area (PA) networks are promoted globally as an effective method of biodiversity conservation and are increasingly implemented to meet the Convention on Biological Diversity Aichi objectives. However, whether PA networks actually conserve biodiversity, and how surrounding landscape features impact their efficacy, has rarely been tested due to their vast size. We used a "landscape mesocosm" approach to test whether functional diversity is maintained locally in PA networks, and whether landscape disturbance in the surrounding matrix detrimentally impacts functional diversity in protected area networks. We measured mammalian biodiversity using camera traps and functional diversity metrics that render our results generalizable to PA networks in working landscapes in ecosystems globally. We used generalized linear models to relate functional diversity to natural, anthropogenic, and protected habitats across a range of 20 spatial scales to encompass increasing amounts of matrix. Functional diversity increased with proportion of natural habitats at small scales and decreased with anthropogenic disturbance at large scales surrounding PA networks. We found the conservation value of a PA network is largely determined by the natural habitat remaining undisturbed, and the degree and type of disturbance in the surrounding working landscape. Implementing protected area networks embedded in degraded ecosystems, without addressing that degradation, will likely not achieve biodiversity conservation goals. To achieve Aichi objectives that transcend cultures, ecosystems, and species, PA networks placed in areas of high natural habitat and mitigated development will provide the best value for biodiversity conservation.

4.3 INTRODUCTION

Protected area (PA) networks – interconnected areas dedicated and managed for the long-term conservation of nature, ecosystem services, and associated cultural values (IUCN 2008) – are increasingly implemented globally, driven by the Convention on Biological Diversity's Aichi Target 11 (CBD 2020). PA networks are a conservation tool hailed as an effective way to conserve biodiversity in the Anthropocene (Bruner et al. 2001, Brooks et al. 2006; Le Saout et al. 2013), and have been implemented across some of the world's most iconic landscapes (*e.g.* North America's Yellowstone to Yukon (Y2Y), Europe's Natura 2000, Western Australia's Macro-Corridor network). However, the assumption that PAs conserve biodiversity is rarely tested (but see Geldmann et al. 2013), and extending this assumption to PA networks is made more difficult by their sheer size. Assuming PAs unambiguously conserve biodiversity – with exception to notable ongoing theoretical arguments (*e.g.* SLOSS; Simberloff

& Abele 1982, Santini et al. 2016) – may have led to the generation of many 'paper parks': PAs that exist for political rather than conservation purposes (Dudley & Stolton 1999; Watson et al. 2014; Di Minin & Toivonen 2015). Empirical evidence of PA network efficiency is needed to prevent development of 'paper networks' under the rapidly approaching CBD 2020 deadline – which would merely multiply the detrimental effects of paper parks across landscapes.

Biodiversity conservation is globally challenged by habitat fragmentation and loss through agriculture, urbanization, and resource extraction (Maxwell et al. 2016). Ongoing landscape change results in increasing prevalence of working landscapes – areas shared by wildlife and by humans, neither pristine wilderness nor urban centers – and are commonly composed of anthropogenic features intermixed with 'natural' features to produce highly heterogeneous spaces (a.k.a. 'human-modified' or 'human-dominated' landscapes; Tscharntke et al. 2012). Despite the increasing prevalence of these landscapes, little is known about their ecological mechanics, (see Amarasekare 2003; Leibold et al. 2004; Tscharntke et al. 2012; Tscharntke et al. 2008), making PA network implementation for effective biodiversity conservation difficult. However, from existing PA networks we can learn how different habitats support species within them, how species distributions vary spatially with natural heterogeneity and anthropogenic disturbance, and how biodiversity is maintained both locally and at larger spatial scales spanning the entire network, and crucially, its surrounding matrix.

To test PA network efficacy, we use a 'landscape mesocosm'. The mesocosm research approach provides a valuable bridge between ecological inferences on small scales (*i.e.* controlled experiments) and the real world (*i.e.* natural systems; Odum 1984). To make widely useful inferences about biodiversity conservation that are relatable among systems, biodiversity needs to be quantified in a generalizable way. Functional diversity metrics (functional richness, evenness, and dispersion) compare the role and position of species within an ecosystem (*i.e.* n-dimensional utilized niche space; Hutchinson 1957). These metrics are translatable among systems (Tilman et al. 1997; Tilman 2001), and better predict ecosystem function than species-based indices (Gagic et al. 2015). Functional richness represents the cumulative roles occupied by all species investigated, functional evenness the uniformity of these roles (see Mason et al. 2005; Villeger et al. 2008 for equations), and functional dispersion the difference between averaged and individual species in their roles (see Laliberte & Legendre 2010 for equations). These generalized measures standardize biodiversity across species and ecosystems, generating biodiversity metrics relatable to ecosystems around the world.

Determining the size of the ecological neighborhoods that affect species – or functional diversity – at a point in space is an unresolved ecological challenge (Pickett & Cadenasso 1995; Wheatley and Johnson 2009). We know that species occurrence at a point in space is affected by more than immediate resources (Fahrig 2001); for example, species integrate information on mates, competitors, and prey from unknown distances away (Zeller et al. 2014). These resources are in turn affected by anthropogenic disturbance (Fahrig 2003). One approach is to model a variety of scales, and determine which scale best fits the collected data (*sensu* Findlay & Houlahan 1997; Fisher et al. 2011; McGarigal et al. 2016). Examining functional diversity-habitat relationships at multiple spatial scales, and across a tractable PA network mesocosm, would (1) identify the best spatial scale to implement PA networks for biodiversity conservation, (2) compare how different habitat features (native vegetation, anthropogenic features, and PA configuration and status) differentially contribute to biodiversity across spatial scales, and (3) provide a reference point for extrapolation of PA network efficacy to other landscapes of varying size and species composition.

As a test of PA network conservation efficacy, we studied a mesocosm PA network as a model for PA networks in working landscapes globally and test the importance of PA implementation, versus measures of landscape composition, across multiple scales. If PA networks within multi-use landscapes are important for biodiversity conservation then functional diversity should increase with both the i) proportion of native vegetation, and ii) proportion, proximity, and conservation status of protected areas, across all spatial scales investigated. Moreover, anthropogenic development in the surrounding landscape should have little to no effect on functional diversity in this scenario. However, if retention or mitigation of native vegetation or anthropogenic features within and among PAs in a network is most important for biodiversity conservation, then there should a stronger relationship to native vegetation variables than to the proportion, proximity, or conservation status of protected areas and functional diversity metrics. We explicitly test the biodiversity conservation value of PA networks and identify the most important features for optimizing their conservation efficiency across landscapes.

4.4 MATERIALS AND METHODS

Most terrestrial protected area networks (PA networks) share some common characteristics: several protected areas of various sizes and degrees of human footprint are spatially clustered within a matrix of unprotected or 'mixed-use' landscape (Dudley & Stolton 1999). The Beaver Hills Biosphere (BHB) is a model mesocosm PA network reflecting this structure, typically manifested in other PA networks over much larger areas, but spanning only 1,596 km². The BHB is a glacial moraine landform supporting trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*) forest with patches of white spruce (*Picea glauca*), open meadows, and small permanent water bodies. Situated in east-central Alberta, Canada (53.381167 °N, 113.062976 °W; Figure 4.1), the BHB has experienced extensive development in the form of timber, and oil and gas extraction, transmission lines, rural residential, and municipal development. The resulting exurban heterogeneous landscape sits in a matrix of agricultural land and is spatially disjunct from tracts of contiguous forests to the north and west (Patriquin 2014).

Hundreds of conservation areas cover the BHB forming a relatively small, but diverse, network of multiple protected areas embedded within a region of high economic value (Figure 4.1). Combined, the landscape hosts a diverse mammal community (Figure 4.2) characteristic of many North American working landscapes. A century of increasing habitat loss and fragmentation for agriculture, paired with ongoing predator persecution (Alberta's Wildlife Predator Compensation Program; see Laliberte & Ripple 2004; Wolf & Ripple 2017 for historic carnivore ranges), has left few top predators, a diversity of mesocarnivores, abundant ungulate species, as well as a variety of species listed as *Sensitive* (fisher, *Pekania pennanti*; American badger, *Taxidea taxus*) or *At-risk* (long-tailed weasel, *Mustela frenata*; Alberta Status Listing 2015) at a provincial level.

To quantify mammalian functional diversity across this heterogeneous protected area network, we used a systematic study design of 4 x 4 km grid cells (64 total; Figure 4.1), which represents a midrange spatial scale for the species we encounter (Fisher et al. 2011). Each cell contained a camera trap (CT; Reconyx[™] models PC85 and PC900) to record multi-species mammal occurrence (Burton et al. 2015). These were positioned to photograph the area surrounding a tree baited with a commercial sent lure (O'Gorman's[™] Long Distance Call) and 5 kg of beaver meat (Fisher & Bradbury 2014; Stewart et al. 2018). Camera traps were deployed for two sampling seasons – January through June 2014, and January through April 2016 – for a total of 10 monthly surveys; bait and lure were replenished at each camera site monthly. All data were collected under Canadian Council of Animal Care permits approved by the University of Alberta Animal Care Committee (AUP00000518).

4.4.1 Quantifying functional diversity metrics

We calculated the relative abundance of each species at each camera site as the number of speciesspecific photos divided by the total number of photos containing an animal of any species. In the R package *FD* (Laliberté et al. 2014), this site-specific species abundance matrix was compared to a functional-trait matrix. From these matrices a functional-trait weighted abundance matrix is created to calculate dissimilarity of different trait types. A principal co-ordinates analysis (PCoA) is then used to compute a functional diversity metric for each site (Laliberté et al. 2014). In mammals, movements can confound abundance metrics (Steenweg et al. 2016; Broadley 2017; Stewart et al. 2018), and body size is related to species-specific scales of habitat selection (Holling 1992; Haskell et al. 2002; Fisher et al. 2011); therefore, we used mammal home-range size and body mass as functional traits within the *FD* analysis (McGill et al. 2006).

4.4.2 Quantifying habitat features across the mesocosm

To test whether protected area (PA) networks explained variance in functional diversity metrics, we used ArcGIS v10.3 (ESRI, Redlands, CA, USA) Geographic Information System to calculate the proportion of habitat features (natural features, anthropogenic features, and PA features; Table 4.1) around camera sites. We used LandSat digital map inventories from the Alberta Biodiversity Monitoring Institute (ABMI; Landcover Map 2014) to quantify the eight primary landcover features in this landscape: water, grassland, shrub-land, cultivation, development, coniferous forest, deciduous forest, and mixed forest. We quantified human footprint variables (ABMI; Human Footprint Map 2014) describing anthropogenic linear features (hard roads, vegetated roads, trails, seismic lines, pipelines, and transmission lines) and anthropogenic block features (rural residential homes and oil well sites). Although there is some spatial dependence between linear, block, and development features, linear features are more spatially continuous within this landscape, and block features distinguish rural-residential homes and well pads from areas of rural-residential development. From the BHB LandSat digital map inventory (Land Management Framework 2015), we quantified aspects of PAs: proportion of area around the camera protected by PAs, legal PA designation (status), and site isolation (measured as the distance of a camera trap to the nearest PA; Table 4.1).

We posited that the effect of PAs on mammalian diversity would diminish with increasing distance. To test this, we quantified habitat (natural features, anthropogenic features, and protected

area features) at multiple spatial scales around each camera. We held the resolution (spatial grain) of habitat features constant and varied the spatial extent at which we quantified habitat around each camera site. We calculated the percent area of all features (Table 4.1) around a camera site within buffers of increasing size, from 250 m – 5,000 m radii in 250 m increments, generating habitat variables at 20 different concentric spatial scales (*sensu* Fisher et al. 2011). Finally, we calculated the percent disturbed landscape (sum of cultivation, development, linear and block features) within a 500 m buffer around each camera site to compare the average amounts of disturbance within each protected area status (Figure 4.3).

4.4.2.1 The importance of protected areas in predicting mammals

To test the hypothesis that the proportion, proximity, and conservation status of protected areas best predict diversity-habitat models, we used model selection to rank three candidate sets of generalized linear models in an information-theoretic framework (Burnham & Anderson 2002). Prior to European colonization, the landscape of the BHB was composed of knob and kettle wetlands, aspen and coniferous forests (Patriquin 2014); given that mammal species native to the area have evolved in response to local conditions – including habitat – we therefore expect that coniferous, deciduous and mixed forested areas, along with water, would be consistently significant features in top models. We also expect management features that ostensibly conserve these native habitats (*i.e.* protected areas) to be related to greater mammalian functional diversity. We therefore predict that the proportion, proximity, and/or conservation status of protected areas will be significant features in all models.

We created three candidate model sets, each with a functional diversity metric as the response, and habitat variables (natural features, anthropogenic features, and protected areas; Table 4.1) measured within a spatial scale as the predictors. Each of the three candidate model sets contained 20 models, one representing each spatial scale. The response variables were assessed for an appropriate probability distribution (*sensu* Zuur 2010). Functional richness was modeled using a gamma family function (inverse link), whereas evenness and dispersion were modeled using Gaussian family functions. We used the *stepAIC* function of the *MASS* package (Ripley et al. 2013), which uses a step-wise procedure that ranks model Akaike Information Criterion values (AIC; Burnham & Anderson 2004) to determine the best-fit model for each spatial scale. Finally, we recorded the consistency of predictor variables across spatial scales. We repeated the above analysis for the occurrence of two guilds of mammals on the Beaver Hills Biosphere; mesocarnivores (red fox, fisher, and coyotes) as well as ungulates (elk, white tailed deer, moose, and mule deer; Figure 4.5)

4.4.2.2 Spatial scales best predicting mammal diversity and occurrence

To determine the best-supported spatial scale explaining mammal functional diversity and guild occurrence, we compared the AIC weights of the best-fit models created at each spatial scale within each candidate model set. The model(s) within a set with the highest AIC weight were identified as the best-supported model, and hence 'characteristic scale' (*sensu* Holland et al. 2004) for predicting mammalian function diversity.

All statistical analyses were performed in R v3.4.2 (R Foundation for Statistical Computing 2017) and we tested for adherence to all model assumptions prior to statistical analyses (*sensu* Zuur 2010). Results are presented as mean ± standard error unless otherwise specified.

4.5 RESULTS

We obtained repeat detections for 15 mammal species across 64 camera sites and 10 months of observations: coyote (*Canis latrans*), fisher (*P. pennanti*), red fox (*Vulpes vulpes*), moose (*Alces alces*), elk (*Cervus canadensis*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), least-, short-, and long-tailed weasel (*M. nivalis*, *M. ermina*, and *M. frenata*), northern flying squirrel (*Glaucomys sabrinus*), red squirrel (*Tamiasciurus hudsonicus*), snowshoe hare (*Lepus americanus*), striped skunk (*Mephitis mephitis*), and porcupine (*Erethizon dorsatum*; Figure 4.2). These detections totaled 137,807 photos over 18,118 camera trap days. On average 2,153 ± 168 mammalian photos were recorded at each camera site. There was no significant correlation between the number of photos recorded at each camera site and the distance of the site to the nearest protected area. More photos were recorded at sites with little disturbance (Pearson correlation: r = -0.28, p = 0.03, df = 62), and at sites on the east side of the study area (Pearson correlation: r = 0.26, p = 0.03, df = 62).

Mammal functional diversity metrics varied among sites (functional richness = 2.81 ± 0.15 , functional evenness = 0.33 ± 0.02 , functional dispersion = 0.82 ± 0.03). Mammal evenness and dispersion were significantly correlated (Pearson correlation; r = 0.56, df = 64, p < 0.0001), whereas mammal richness was not correlated with either mammalian evenness (Spearman rank correlation; rho = -0.11, df = 64, p = 0.38) or mammalian dispersion (Spearman rank correlation; rho = 0.15, df = 64, p = 0.23).

4.5.1 Protected areas rarely explain mammal functional diversity

The BHB mesocosm is composed of 763 PAs, which range in size from multiple small conservation easements at 1.2 m² up to Elk Island National Park at 134,464.5 km² (mean = 784.1 km² ± 290 km²; Figure 4.1). Despite this substantial and complex network, we determined that protected areas rarely explained observed functional diversity metrics. The exception is for functional dispersion at large scales: at small scales species are similar in their ecological roles, whereas at large spatial scales species differentiate their ecological roles the farther sites are from protected areas, although this effect was not significant (Figure 4.4B).

4.5.2 Local natural features promote functional diversity and distant anthropogenic features suppress it

Natural features generally have a positive relationship with functional diversity metrics across all spatial scales (Figure 4.4A-C). Natural features best explain functional diversity at small scales (scales < 2000 m), and these are generally positive relationships: functional evenness significantly increases with deciduous and coniferous forests at small scales (Figure 4.4C) and are also important for functional dispersion (Figure 4.4B) and richness (Figure 4.4A).

Anthropogenic features generally have a negative relationship with functional diversity metrics across all spatial scales, the exception being linear features at some small (Figure 4.4C) and intermediate scales (Figure 4.4B). Anthropogenic features best predict functional diversity at large scales (scales > 2000m), and these are generally negative relationships: functional richness decreases with linear features (Figure 4.4A), functional dispersion decreases with development (Figure 4.4B), and functional evenness decreases with both cultivation and development (Figure 4.4C).

4.5.3 Mammal functional diversity is explained by both near and distant landscape features

No single scale best explains functional evenness, diversity, or richness diversity metrics. Model AIC weights were spread more or less evenly across all scales of mammal diversity, with no model

explaining more than 25% of the weight of evidence (Figure 4.4A-C). Best-fit models carrying the most weight of evidence were 4250 m for functional richness (AIC_w = 12%, null deviance = 27.97, df = 61 df; residual deviance = 27.95, df = 60), 3500 m for functional dispersion (AIC_w = 21%, null deviance = 4.55, df = 63; residual deviance = 3.69, df = 59), and 500 m for functional evenness (AIC_w = 25%, null deviance = 1.24, df = 63; residual deviance = 1.03, df = 61). It appears landscape features near to, and farther from, camera sites were equally important in explaining mammalian functional diversity.

4.6 DISCUSSION

Protected areas (PAs) are not significant predictors of mammal functional diversity across the BHB's PA mesocosm. Instead, the matrix in which the PAs are embedded play a key role in explaining functional diversity. Across the PA network we studied, a combination of natural and anthropogenic features best explains functional diversity and features up to 5 km away were as important as features close by: what happens outside of protected areas, affects biodiversity inside protected areas. We found within this PA network what others have found for single PAs: habitat features surrounding PAs are critical to their function (DeFries et al. 2010; Leroux & Kerr 2013). For PA networks to conserve biodiversity, the working landscape between PAs must also work to maintain biodiversity.

4.6.1 Protected area networks and biodiversity conservation

The value of PAs within a network is dependent on the composition and configuration of the surrounding landscape. As a result, the effective area of a PA network might be either larger, or smaller, than what is mapped (Weins 2009; DeFries et al. 2010), depending on the value of that matrix (Driscoll et al. 2014). Baker (2016) found that the effective carnivore conservation area of three parks in the southern United States was much smaller than mapped – all carnivores avoided the edge of the protected areas and were sensitive to human disturbance within protected areas. The conservation value of new PAs, either as stand-alone areas or as components of a PA network, is therefore dependent on the natural and anthropogenic features in the surrounding landscape.

The escalating extent and density of global anthropogenic disturbance makes landscapes with high habitat loss and fragmentation increasingly abundant (Foley et al. 2005). These landscapes frequently experience a "ghost of predation past", where large predators have experienced persecution from human-wildlife conflict (Berger 1999; Woodroffe et al. 2005) or range contraction correlated with post-European settlement (Laliberte & Ripple 2006). Our study takes place on such a landscape and is therefore relevant to many landscapes being considered for PA networks. Globally, only 3.6% of mammalian geographic ranges are situated in highly suitable habitat within protected areas – the other 96.4% are in areas of high anthropogenic disturbance. This disturbance is directly related to extinction risk (Crooks et al. 2017), where both protected areas, and the landscape surrounding them, need to be better managed to improve natural habitats (DeFries et al. 2010) . For example, Shackelford et al. (2017) found evidence for a trade-off between mammalian conservation and development at large spatial scales. Our research highlights the fact that managers need to be considering land use decisions at all spatial scales to prevent significant species extinctions in the face of rapid landscape change.

4.6.2 Processes moderating biodiversity in working landscapes

Ecological processes change among spatial scales (Wiens 1989; Dunning 1992; Holling 1992; Levins 1992; Liebold et al. 2004; Tscharntke et al. 2012), and hence so do biodiversity-habitat relationships (Fahrig 2003; Hewitt et al. 2010). The consistency of AIC weights between our scale models (Figure 4.4A-C) demonstrates the importance of considering multiple scales when implementing PA networks within landscapes: neither small nor large scales were more important for explaining functional diversity. At small scales, natural habitat is the most important factor for conserving biodiversity; at larger scales mitigating anthropogenic features is the most important. Foundational theoretical research predicts this divide between biotic and abiotic process governing ecological patterns at small vs. large scales (summarized in Tscharntke et al. 2012), and are consistent with our findings; at large scales, abiotic features override local interacting biotic features, and this divide can be amplified when measured at the community level (Ricklefs 1987). We contend landscape-scale anthropogenic features might be overriding local natural features – whether within or between PAs – that are beneficial to biodiversity.

Alternatively, either (1) beta diversity, and or (2) landscape-moderated functional trait selection (Tscharntke et al. 2012), may be moderating biodiversity-habitat relationships with the BHB mesocosm. The dissimilarity of local communities across the BHB may determine the landscape scale biodiversity patterns and override potential negative relationships between biodiversity and habitat fragmentation, habitat loss, or anthropogenic features at local scales (Tscharntke et al. 2012). For example, in an elegant example of controlled habitat loss and habitat fragmentation, Rubene et al. (2015) found that beta diversity best predicted local wild bee and wasp species richness when compared to either habitat

loss or fragmentation. In a similar conclusion to ours, they inferred that conservation efforts are most effective when applied at multiple spatial scales. However, landscapes can also moderate the functional traits of species; this moderation can shape the functional role of species occurring at smaller scales within the landscape (Tscharntke et al. 2012) and may be moderating the functional diversity-habitat relationships observed on the BHB mesocosm. Gamez-Virues et al. (2015) highlight the importance of a diversity of landcover types at landscape scales for maintaining diverse functional traits at local scales. They show the simplification of landscapes by agriculture (especially monocultures) filters out functional traits at both local and landscape scales, and that this 'biotic homogenization' is a significant contributor to biodiversity decline.

4.6.3 Recommendations for future conservation

Newly implemented protected areas will have the highest biodiversity conservation value if (1) placed in landscapes with little anthropogenic disturbance, or (2) are accompanied by significant restoration efforts in the surrounding working landscape matrix. To be effective, conserving natural features and mitigating anthropogenic disturbance within and around protected area networks is required. More importantly, managing anthropogenic footprint between protected areas will increase the conservation value of existing, as well as new, protected area networks. Although important components of conservation, protected area networks are not a stop-gap fix within already disturbed landscapes; landuse decisions must prioritize conserving natural features across working landscapes (not just protected areas) to avoid extending the ineffectiveness of 'paper parks' into 'paper networks'.

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4.2 TABLES AND FIGURES

Table 4.1 Habitat features hypothesized to explain mammal diversity across the Beaver Hills Biosphere mesocosm

Category	Habitat features	Description
Natural features	Deciduous forest	Proportion of deciduous forest; native natural forest stands of primarily aspen or balsam poplar
	Coniferous forest	Proportion of coniferous forest; native natural forest stands of primarily white or black spruce
	Mixed wood forest	Proportion of mixed wood forest; native natural forest stands of both deciduous and coniferous
	Wetlands	Proportion of water bodies; wetlands, lakes, and streams
	Grassland	Proportion of grassland; native natural grass cover
	Shrub-land	Proportion of shrub-land; native natural shrub cover
Anthropogenic	Linear	Proportion of linear features; linear human footprint (e.g. hard roads, vegetated roads,
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features		trails, seismic lines, pipelines, and transmission lines)
	Block	Proportion of block features; blocks of human footprint (e.g. well pads and rural residential)
	Cultivation	Proportion of cultivation; cultivated agricultural lands
	Development	Proportion of development; residential – industrial lands (e.g. current country- residential and industrial developments; does not include rural-residential components of Block features)
Protected areas	Protected Area	Proportion of protected areas; protected area of any status (e.g. public lands, provincial parks, provincial recreation areas, national parks, conservation areas, and NGO sites)
	Status	
		Status of land protection at each camera site location: 0 – Private land, 1 –
		Public/county lands, 2 - Provincial conservation land, 3 - National park, 4 -
		Provincial recreation land, 5 – Non-governmental organization lands
	Distance	
		Proximity of a camera site to the nearest protected area.



Figure 4.1 Sixty-four wildlife camera sites were deployed across protected areas within the Beaver Hills Biodiversity network (black dot, inset) of east-central Alberta, Canada. Large national parks, and provincial parks and recreation conservation lands are identified. All smaller protected areas represent public/county lands or Non-government organization lands. Private lands (i.e. the working landscape matrix) are in white.



/ildlife cameras documented repeat occurrences of (a) while tailed deer, (b) mule deer, (c) elk, (d) moose, (e) fisher, (f) coyote, (g) long-tailed weasel, (h) sort-tailed weasel, (i) snowshoe hare, (j) striped skunk, (k) porcupine, (l) red fox, as well as red squirrels, northern flying squirrels, and least weasels.



Figure 4.3 The averaged percent disturbed landscape (cultivation, development, linear and block features) within a 500-m buffer of camera sites grouped by protected area status. Statuses refer to 0 – private land, 1 – public/county lands, 2 – Provincial conservation lands, 3 – National Parks, 4 – Provincial recreation lands, and 5 – Non-government organization lands. Bars and whiskers represent means +/- standard errors, and numbers above bars represent the number of camera sites (N) within each type of protected area.











Figure 4.4 Across a heterogeneous working landscape, mammal functional richness (A), dispersion (B), and evenness (C) were best predicted by positive relationships with natural features at small scales, and negative relationships with anthropogenic features at large scales. When compared across spatial scales, model AIC weights were similar and demonstrate the importance of considering biodiversity-habitat relationships at all scales when implementing conservation and management strategies.



Figure 4.5 Guild specific scales of habitat selection for both mesocarnivores (fisher, coyotes, and red foxes) and unglulates (white tailed deer, mule deer, elk, and moose) on the Beaver Hills Biosphere. Best fit scales of habitat selection are indicated by high AIC weights. No scale was the only best fit for these guilds, as represented by AIC weights less than 20%. However, mesocarnivores generally select habitat at the 750m scale, while ungulates generally select habitat at the 1000-1500m scales.





Figure 4.6 Species specific camera detection rates (# species photos/# camera days) are shown by increasing blue bubble sizes across all 64 camera trapping sites that were part of the Moraine Mesocarnivore Project (2014-2016). Sizes of bubbles represent the relative abundance of species across the Beaver Hills Biosphere; bubble size is not comparable between graphs. Numbers represent each camera trapping site.

LTweasel refers to long-tailed weasel. Lweasel refers to least weasel. MD refers to Mule deer. STweasel refers to Short-tailed weasel. WTD refers to white tailed deer.