



# Protected areas alone rarely predict mammalian biodiversity across spatial scales in an Albertan working landscape



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## ABSTRACT

Protected areas (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, is controversial. We used a landscape approach to test whether mammalian biodiversity is maintained locally in PA networks, and whether landscape disturbance in the surrounding matrix detrimentally impacts biodiversity. We measured mammalian biodiversity using camera traps and functional diversity metrics, an approach that could be broadly applied to PA networks in working landscapes globally. We used generalized linear models to relate mammalian biodiversity metrics to natural, anthropogenic, and protected habitats across a range of 20 spatial scales to encompass increasing amounts of matrix. Biodiversity metrics increased with proportion of natural habitats at small scales and decreased with anthropogenic disturbance at large scales surrounding PAs. We found the conservation value of PAs are largely determined by the natural habitat remaining undisturbed, and the degree and type of disturbance in the surrounding working landscape. Implementing protected areas in degraded ecosystems, without addressing that degradation, will likely not achieve mammalian biodiversity conservation goals. We suggest, to achieve Aichi objectives, PAs placed in areas of high natural habitat and mitigated development will provide the best value for mammalian biodiversity conservation.

## 1. Introduction

Protected areas (PAs) – areas dedicated and managed for the long-term conservation of nature, ecosystem services, and associated cultural values (IUCN, 2008) – are implemented globally. PAs 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 PA networks 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 Wiersma and Simonson, 2010; Geldmann et al., 2013); testing this assumption is often hampered by the sheer size of protected area networks, and a limited sample size of

independent PA units. PAs come in many different forms, not all of which have the conservation of biodiversity as a priority; many PAs exist for political (Dudley and Stolton, 1999; Watson et al., 2014; Di Minin and Toivonen, 2015), economic, or aesthetic rather than conservation purposes.

Biodiversity conservation is globally challenged by habitat fragmentation and loss through agriculture, urbanization, and resource extraction (Hobbs, 1997; 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,

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little is known about their ecological mechanics, (see Amarasekare, 2003; Leibold et al., 2004; Tscharntke et al., 2012, 2008), making PA implementation for effective biodiversity conservation difficult. To plan effective PAs, designs need to understand how the types and intensity of land use and habitat, both within and around PAs, affect their conservation efficacy (Wiersma et al., 2004). From existing combinations of PAs we can learn how different habitats support species within them and how species distributions vary spatially with natural heterogeneity and anthropogenic disturbance; we can infer how biodiversity is maintained both locally and at larger spatial scales spanning the entire landscape, and crucially, its imbedded matrix.

To test PA efficacy, we use an exemplar mosaic landscape that comprises components of many working landscapes globally. A tractable landscape, with a PA network embedded, provides a valuable bridge between ecological inferences on small scales (i.e. privately owned small plots of land, or small conservation easements) and the potential for regional protection (i.e. Yellowstone to Yukon, Natura 2000). 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). 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 Laliberté & 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 and 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), and across multiple habitat-specific scales (Laforge et al., 2015). 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 and Houlahan, 1997; Fisher et al., 2011; LaForge et al., 2015;). Examining functional diversity- habitat relationships at multiple spatial scales, and across a tractable exemplar landscape composed of a PA network of varying sizes and statuses embedded in different contexts would be effective in several ways. It would (1) identify the best spatial scale to implement PAs for biodiversity conservation, (2) compare how different, and non-mutually exclusive, habitat features (native vegetation, anthropogenic features, and PA configuration and status) differentially contribute to biodiversity across spatial scales, and (3) provide a generalizable example for extrapolation of PA efficacy to other working landscapes of varying size and species composition.

As a test of PA conservation efficacy, we model mammalian functional diversity and occurrence across a suite of PAs and its surrounding landscape. We investigated 20 spatial extents ranging from very small, local effects (250-m radius) to large, landscape effects (5-km radius). If PAs within multi-use landscapes are important for mammal conservation then mammalian biodiversity and occurrence should increase with both i) the proportion of native vegetation, and ii) the proportion, proximity, and conservation status of protected areas, across all spatial scales investigated. Moreover, where PAs are present on the landscape, we would expect them to explain most of the variation in mammal biodiversity, with anthropogenic development playing a comparatively minor role. However, if retention of native vegetation within and

among PAs is most important for mammalian biodiversity conservation, then there should be a stronger relationship to native vegetation variables than to the proportion, proximity, or conservation status of protected areas and biodiversity metrics. Conversely, if anthropogenic development within and around PAs negatively affects mammalian biodiversity, these variables should best explain variation in biodiversity, especially at larger spatial extents. We explicitly test the value of PAs for mammal conservation and identify the most important features for optimizing their conservation efficiency across working landscapes.

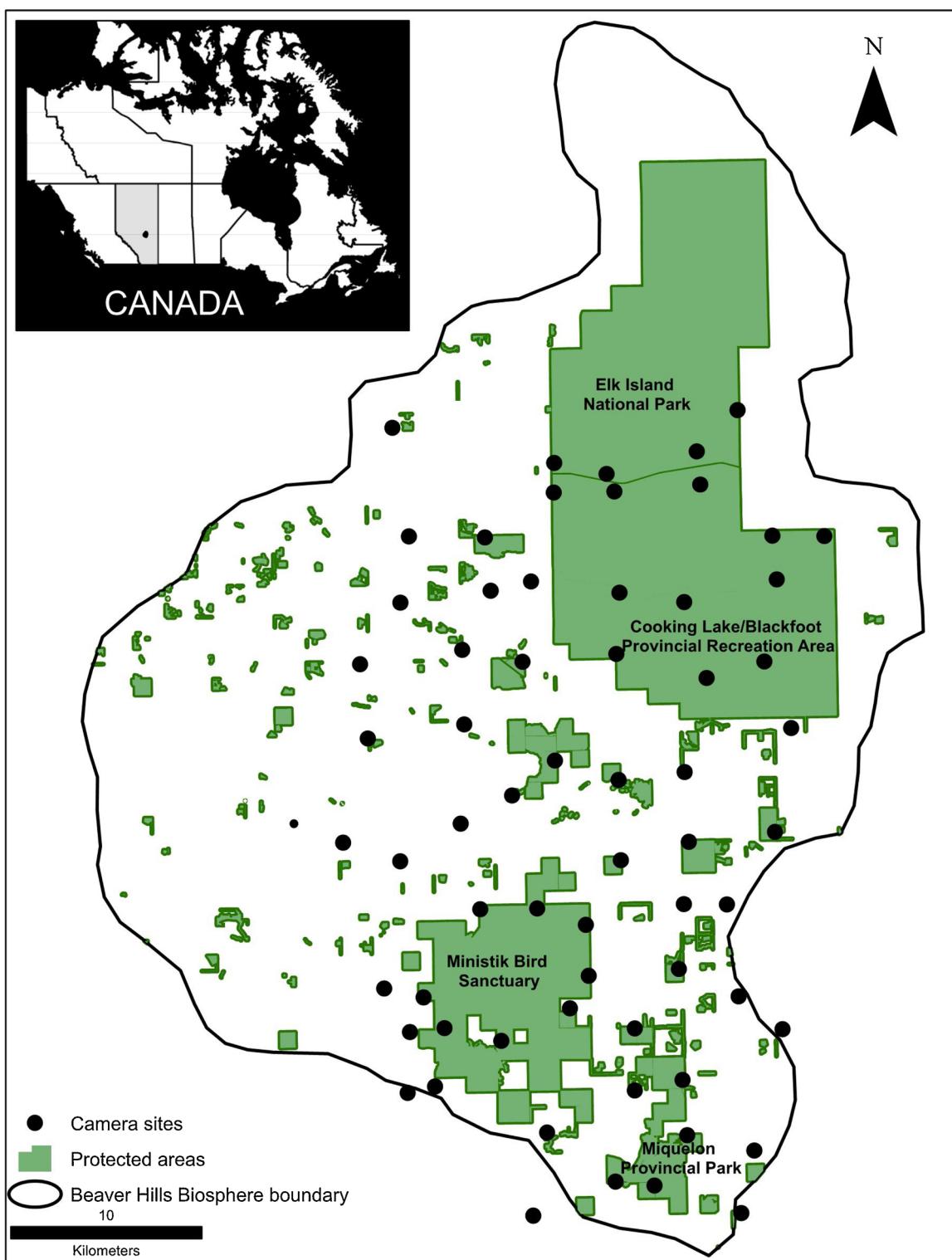
## 2. Methods

### 2.1. Data collection across an example landscape

Most terrestrial protected area (PA) networks share some common characteristics: several protected areas of various sizes, degrees of human footprint, and management strategies are spatially clustered within a matrix of unprotected or ‘mixed-use’ landscape (Dudley and Stolton, 1999). The Beaver Hills Biosphere (BHB) is an exemplar mosaic working landscape reflecting this structure, typically manifested in other PA networks over much larger areas, but spanning only 1,596 km<sup>2</sup>. 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; Fig. 1), the BHB has experienced development in the form of forestry, oil and gas extraction, transmission lines, rural residential, and municipal development. The resulting 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).

The BHB forms a relatively small, but diverse, landscape composed of multiple protected areas embedded within a region of high economic value (Fig. 1). Combined, the landscape hosts a diverse mammal community (Fig. 2) characteristic of many North American working landscapes (Laliberte and Ripple, 2004). A century of increasing habitat loss and fragmentation by agriculture, paired with ongoing predator persecution (e.g. Alberta's Wildlife Predator Compensation Program; see Wolf and 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. The PAs include one fenced National Park which rears Bison (*Bison bison bison*, and *B. b. athabasca*; Elk Island National Park), a Provincial recreation area that allows cattle grazing (Cooking-Lake Blackfoot Recreation Area), intermixed with a suite of smaller areas with varying land use histories. This diverse system of PAs represents a continuum of management strategies that can be encompassed by the PA's status (Fig. 2).

To quantify mammalian biodiversity – which includes generalists and specialists – across this heterogeneous protected area network, we used a systematic study design of 4 x 4 km grid cells (64 total; Fig. 1). This cell size represents a grain that is mid-range for the species we encounter (Fisher et al., 2011; Stewart et al. 2019; Burgar et al., 2018). 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 and Bradbury, 2014; Stewart et al., 2018; Stewart et al., 2019a). 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).



**Fig. 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.

## 2.2. Quantifying biodiversity: functional diversity metrics and species occurrence

We calculated the relative abundance of each species at each camera site as the number of species-specific photos divided by the total number of photos containing an animal of any species (*sensu* Burton et al., 2015). In the R package (R Foundation for Statistical Computing,

2017) FD (Laliberté et al., 2014), this site-specific species abundance matrix was combined with a functional-trait matrix (Table A1.1). 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 constructed a functional-trait matrix that included both the species specific home-



**Fig. 2.** Wildlife cameras documented repeat occurrences of (a) white 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.

range size and body mass of each mammal species used in this analysis (15 species; Fig. 2; Appendix 1). The smallest mammal species were weasels (*Mustela* sp.). We removed all domesticated species, including bison, from this analysis.

From these two matrices – 1. the relative abundance of each species at each study site as summarized from camera trapping data, and 2. the species-specific home-range size and body mass as summarized from literature - a functional-trait weighted abundance matrix was created within the *FD* package. The *FD* package conducts a principal co-ordinates analysis (PCoA) on this matrix to compute a functional diversity metric for each camera site (see Laliberté et al., 2014 for exact computation). This analysis compressed the relative abundance, body mass, and relative home-range size of each mammal species across 64 camera sites into three diversity metrics for each camera site – functional richness ( $N = 64$ ), functional evenness ( $N = 64$ ), and functional

diversity ( $N = 64$ ). Additionally, to investigate species-specific responses to natural, anthropogenic, and protected area landscape features, we quantified species occurrence as a monthly count (0–10) at each camera site ( $N = 64$ ).

### 2.3. Quantifying the landscape: habitat features within and between protected areas

To test whether protected areas (PAs) 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 overlaid PA features; Table 1) at 20 spatial extents around camera sites. We used LandSat digital map inventories from the Alberta Biodiversity Monitoring Institute (ABMI; Landcover Map 2014) to quantify the eight

**Table 1**

Categories of habitat features hypothesized to explain mammal diversity across the Beaver Hills Biosphere. Protected areas were non-mutually exclusive from both natural and anthropogenic features.

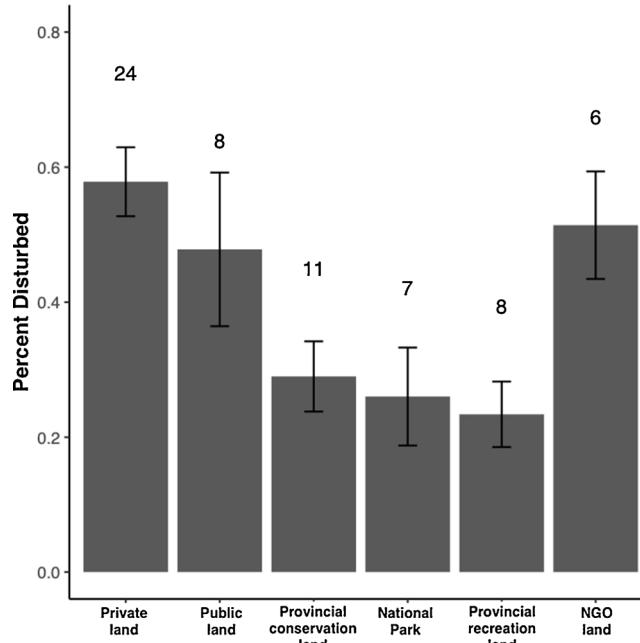
Category	Habitat features	Description
Natural features	Deciduous forest	Proportion of deciduous forest; native natural forest stands of primarily aspen or balsam poplar
	Coniferous forest	Proportion of coniferous forest; native natural forest stands of primarily white or black spruce
	Mixed wood forest	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 features	Linear	Proportion of linear features; linear human footprint (e.g. hard roads, vegetated roads, 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 Status	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)
	Distance	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
		Proximity of a camera site to the nearest protected area.

primary landcover features within and between the protected areas of this landscape: water, grassland, shrub-land, cultivation, development, coniferous forest, deciduous forest, and mixed forest. We also 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) within and between protected areas. 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, we quantified characteristics of PAs: proportion of area around the camera site protected by PAs, legal PA designation (status), and site isolation (measured as the distance (m) of a camera trap to the nearest PA; Table 1). These predictor variables were standardized using the *scale* function in R.

To test the effect of spatial extent on landscape-functional diversity relationships we modelled the three functional diversity metrics against natural features, anthropogenic features, and protected area features around each camera. We held the resolution (spatial grain) of habitat features constant and buffered each camera site by 20 spatial extents, calculating the proportion area of all features (Table 1) within buffers from 250 m – 5,000 m radii in 250 m increments (*sensu* Fisher et al., 2011). Finally, we calculated the proportion of disturbed landscape (sum of cultivation, development, linear and block features divided by all other natural/anthropogenic landscape features) within a 500 m buffer around each camera site to quantify the average amounts of disturbance within each protected area status (Fig. 3).

### 2.3.1. The importance of protected areas in predicting mammalian biodiversity

To test the hypothesis that the proportion, proximity, and conservation status of protected areas best predict diversity-habitat relationships, we used model selection to rank candidate sets of generalized linear models in an information-theoretic framework (Burnham and 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 consistently be 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 and mammal

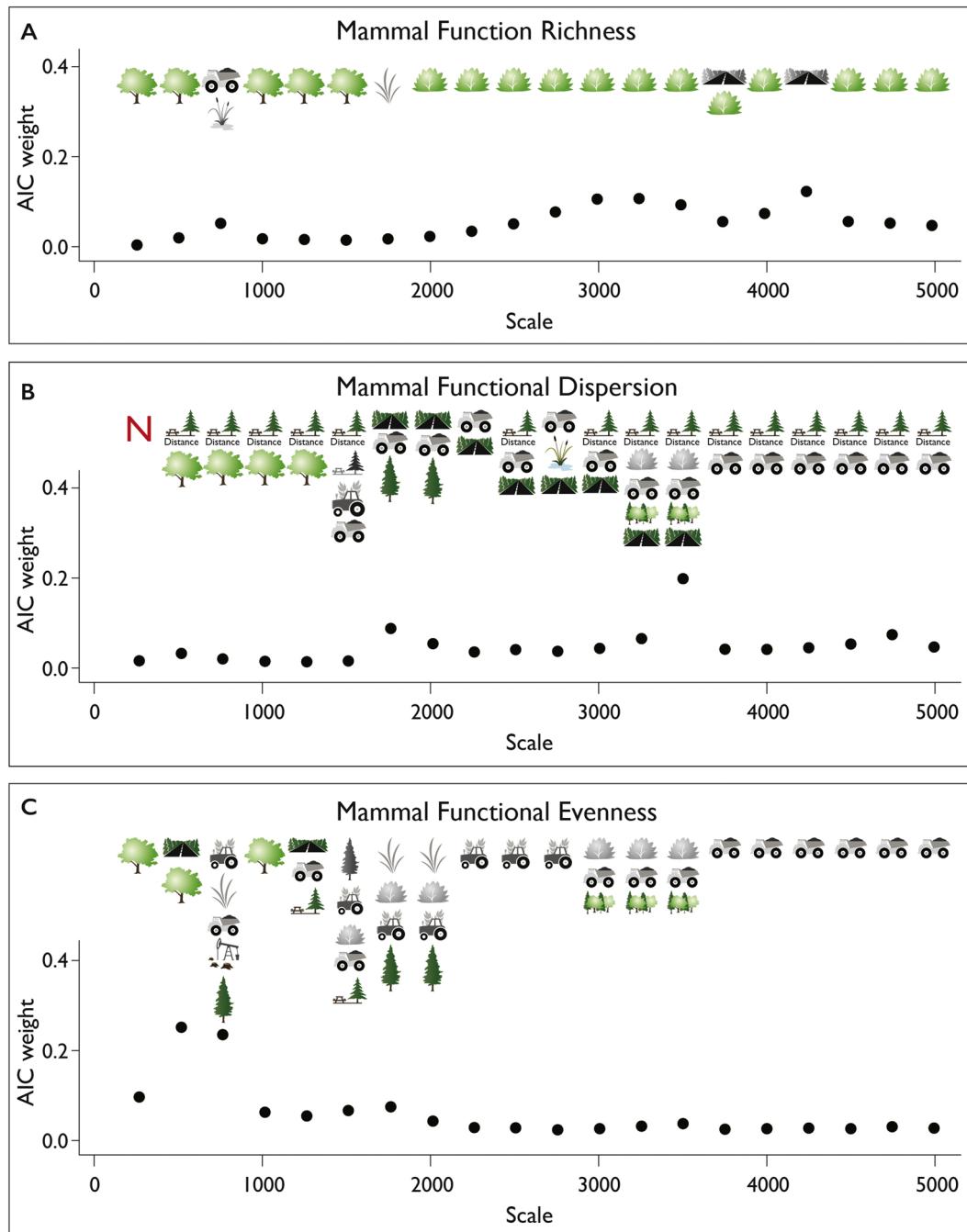
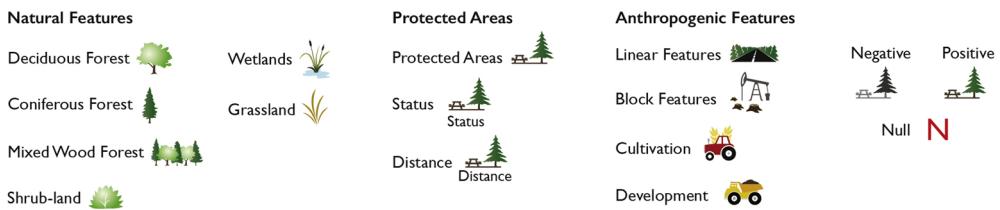


**Fig. 3.** The averaged percent of disturbed landscape (cultivation, development, linear and block features) within a 500-m buffer of camera sites grouped by protected area status. Statuses include private land, public/county lands, Provincial conservation lands, National Parks, Provincial recreation lands, and 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.

occurrence. 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 for our diversity metrics: one each for functional diversity, functional richness, and functional evenness. Each candidate set contained twenty models. In each model, we modelled the diversity metric against habitat variables – natural features, anthropogenic features, and protected areas (Table 1) – measured at one of the twenty spatial scales. We performed the same procedure for our occurrence metrics: one occurrence metric for each species across a candidate set of twenty models. We modeled our occurrence metric against habitat variables (Table 1) measured at one of twenty spatial scales. The model construct and error structure for each

### Legend



**Fig. 4.** Across a heterogeneous working landscape, mammal functional richness (A), dispersion (B), and evenness (C) were best predicted by positive (coloured) relationships with natural features at small scales, and negative (greyscale) 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.

candidate set were determined by the distribution of the response variable (*sensu* Zuur et al., 2010): functional richness was modeled using a gamma function (inverse link), evenness and dispersion were modeled using Gaussian functions, and occurrence was modeled using a posisson function (log link). 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 and Anderson, 2004) to determine the most parsimonious model for each spatial scale – a form of analysis suitable when there are no *a priori* hypotheses available and that produces models that perform as well as other model selection algorithms (Murtaugh, 2009). Finally, we plotted the best-supported predictor variables across spatial scales.

### 2.3.2. Spatial scales best predicting mammalian biodiversity and occurrence

To determine the best-supported spatial scale explaining mammal functional diversity and species-specific occurrence, we compared the AIC weights of the best-supported models 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 functional diversity or occurrence (*sensu* Fisher et al., 2011).

All statistical analyses were performed in R v3.4.2 and we tested for adherence to all model assumptions prior to statistical analyses (*sensu* Zuur et al., 2010). Results are presented as mean  $\pm$  standard error unless otherwise specified.

## 3. 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. erminea*, and *M. frenata*), northern flying squirrel (*Glaucomys sabrinus*), red squirrel (*Tamiasciurus hudsonicus*), snowshoe hare (*Lepus americanus*), striped skunk (*Mephitis mephitis*), and porcupine (*Erethizon dorsatum*; Fig. 2). These detections totaled 137,807 photos over 18,118 camera trap days. On average  $2,153 \pm 168$  mammal 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:  $r = 0.26$ ,  $p = 0.03$ ,  $df = 62$ ). We obtained the most photos from coyote, fisher, red fox, red squirrel, flying squirrel, moose, white tailed deer, mule deer, and snowshoe hare.

Mammal functional diversity metrics varied among sites (functional richness =  $2.81 \pm 0.15$ , functional evenness =  $0.33 \pm 0.02$ , functional dispersion =  $0.82 \pm 0.03$ ). Mammal evenness and dispersion were significantly correlated (Pearson correlation;  $r = 0.56$ ,  $df = 64$ ,  $p < 0.0001$ ) – demonstrating functional role uniformity varies positively with functional role differentiation – 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 =  $0.15$ ,  $df = 64$ ,  $p = 0.23$ ).

### 3.1. Protected areas alone rarely explain mammalian biodiversity or mammal occurrence

The BHB landscape is composed of 763 PAs, which range in size from multiple small conservation easements ( $100 \text{ m}^2$ ) up to Elk Island National Park at  $194 \text{ km}^2$  (Fig. 1). Despite this substantial and complex network, we determined that protected areas alone rarely explained observed functional diversity metrics. The exception is for functional dispersion at large scales: at large scales, functional dispersion increased with distance from a PA, and at small scales there was little to

no effect (Fig. 4B).

Nine of the 15 mammal species studied here had the required data density to ensure convergence of species-specific models. We found that protected areas were positively associated with only two of these nine species: northern flying squirrel at a spatial scale of 1250 m, and mule deer at a spatial scale of 2500 m. Protected areas were negatively associated with the occurrence of two species: fisher at a spatial scale of 1750 m, and red fox at a spatial scale of 500 m. Finally, protected areas were not associated with five of the nine species investigated: coyote at a spatial scale of 4750 m, moose at a spatial scale of 250 m, red squirrel at a spatial scale of 4650 m, snowshoe hare at a spatial scale of 4500 m, and white tailed deer at a spatial scale of 5000 m (Appendix 2).

### 3.2. Local natural features promote mammalian biodiversity and distant anthropogenic features suppress it

Natural features generally have a positive relationship with functional diversity metrics across all spatial scales (Fig. 4A–C; Table A1.2). Natural features best explain functional diversity at small scales (scales  $< 2000 \text{ m}$ ), and these are generally positive relationships: functional evenness significantly increases with the proportion of deciduous and coniferous forests at small scales (Fig. 4C) and are also important for functional dispersion (Fig. 4B) and richness (Fig. 4A).

Anthropogenic features generally have a negative relationship with functional diversity metrics across all spatial scales, the exception being linear features at some small (Fig. 4C) and intermediate scales (Fig. 4B). Anthropogenic features best predict functional diversity at large scales (scales  $> 2000 \text{ m}$ ), and these are generally negative relationships: functional richness decreases with linear features (Fig. 4A), functional dispersion decreases with development (Fig. 4B), and functional evenness decreases with both cultivation and development (Fig. 4C).

### 3.3. Mammalian biodiversity 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 (Fig. 4A–C; Table A1.2). For our functional richness measure, the model at the 4250 m scale, with linear features as the predictor, had the highest weight of evidence when compared against all other functional richness models ( $AIC_W = 12\%$ , null deviance = 27.97,  $df = 61$  df; residual deviance = 27.95,  $df = 60$ ). For functional dispersion, the model at the 3500 m scale, with linear features, deciduous forest, development, shrubs, and distance to PAs as predictors, had the highest weight of evidence when compared against all other functional dispersion models ( $AIC_W = 21\%$ , null deviance = 4.55,  $df = 63$ ; residual deviance = 3.69,  $df = 59$ ). For functional evenness the model at the 500 m scale, with deciduous forest and linear features as the predictors, had the highest weight of evidence when compared to all other functional evenness models ( $AIC_W = 25\%$ , null deviance = 1.24,  $df = 63$ ; residual deviance = 1.03,  $df = 61$ ); Fig. 4; Table A1.2). Although the AIC weights for any single spatial scale are low, the consistency across scales provides a cumulative weight of evidence that landscape features near to, and farther from, camera sites were equally important in explaining mammalian functional diversity.

## 4. Discussion

Protected areas (PAs) alone are not significant predictors of mammalian biodiversity or occurrence across the BHB working landscape. Instead the matrix, in which PAs are embedded, plays a key role in explaining biodiversity. Across the PA network we studied, a combination of natural and anthropogenic features best explains three functional biodiversity metrics despite the presence, status, and distance of

sampling sites from PAs. 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 across multiple PAs what others have found for single PAs: habitat features surrounding PAs are critical to their function (DeFries et al., 2010; Leroux and Kerr, 2013). For combinations of PA to conserve biodiversity across spatial scales (e.g. networks of PAs), the working landscape between PAs must also work to maintain biodiversity.

#### 4.1. Implications for PA networks

The value of individual 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 (, Wiersma et al., 2004; DeFries et al., 2010), depending on the value of the 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. Wiersma et al. (2004) found that habitat within 50 km of Canadian park boundaries is important for mammal species conservation within PAs. The conservation value of new PAs, either as stand-alone areas or as components of a PA network, is therefore dependent on both natural and anthropogenic features in the surrounding landscape.

Studying a PA network on any specific landscape will provide generalities to other landscapes, while suffering exigencies that make inference to other landscapes problematic. The PAs within the working landscape studied here are representative of many such areas governed directly, or indirectly, by anthropogenic change (Hobbs, 1997) – areas of high fragmentation, with interspersed natural and anthropogenic features (Tscharntke et al., 2012) – that now exceed the area of undeveloped landscapes globally (Watson et al., 2014). As such, PAs must perform a demanding task; they are expected to anchor biodiversity amongst escalating anthropogenic disturbances at both local, and global, scales (Rodrigues et al., 2004; Chape et al., 2005; Foley et al.,). However, extrapolating the effects of one landscape (*i.e.* local scale), to regional and global scales, has been a long-standing and ongoing topic of debate in landscape ecology (Hargrove and Pickering, 1992; Davies and Grey, 2015; Barley et al., 2017). Landscape studies need not be ‘replicated’ to provide a general understanding between a system and its environment (Hargrove and Pickering, 1992); hypothesis-driven studies of a single landscape can provide a productive research avenue to offer generalities at larger scales (Hobbs, 1997). Although no landscape can supply a perfect location for ecological inference, landscapes relevant to contemporary change, and studies that investigate multiple spatial scales are a good place to start (Hobbs et al., 1997; Tscharntke et al., 2012). Here we use a landscape with many similarities to an increasingly abundant landscape type globally to discriminate among hypotheses at multiple spatial scales, and infer processes maintaining biodiversity at larger extents.

Globally, landscapes with high habitat loss and fragmentation 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 (é & Ripple,). 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 land use change.

#### 4.2. Understanding the processes moderating biodiversity in working landscapes

Ecological processes change among spatial scales (Wiens, 1989; Holling, 1992; Levin, 1992; 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 (Fig. 4A–C; Table A1.2) 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-modulated functional trait selection (Tscharntke et al., 2012), may be moderating biodiversity-habitat relationships within the BHB. 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 landscape. 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.

#### 4.3. Local and global considerations for protected areas and conservation

In light of the 2020 Aichi targets (CBD, 2010), we suggest newly implemented protected areas will have the highest mammalian 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 panacea wherein we eliminate the negative effects of disturbance elsewhere by establishing a protected area. Land use decisions must prioritize conserving natural features across working landscapes (not just legally established protected areas) to avoid amplifying the ineffectiveness of ‘paper parks’ (Dudley and Stolton, 1999; Watson et al., 2014; Di Minin and Toivonen, 2015; Coad et al., 2019;

[Stewart et al. 2019b](#)) into ‘paper networks’.

## Declaration of Competing Interest

The authors have no conflict of interest to declare.

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## Further Reading

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