



Community-level modelling of boreal forest mammal distribution in an oil sands landscape

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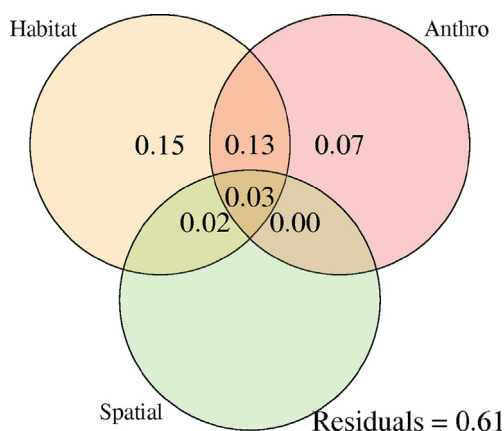
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HIGHLIGHTS

- Industry development best predicts predator relative use of the boreal forest.
- Both linear and non-linear anthropogenic features are relevant for conservation.
- Natural and anthropogenic variables affect prey and predators at different scales.

GRAPHICAL ABSTRACT



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ABSTRACT

Anthropogenic landscape disturbances are known to alter, destroy, and fragment habitat, which typically leads to biodiversity loss. The effects of landscape disturbance generally vary among species and depend on the nature of the disturbances, which may interact and result in synergistic effects. Western Canada's oil sands region experiences disturbances from forestry and energy sector activities as well as municipal and transportation infrastructure. The effects of those disturbances on single species have been studied and have been implicated in declines of the boreal woodland caribou (*Rangifer tarandus caribou*). Yet, the specific responses of the mammal community, and of functional groups such as prey and predators, to those interacting disturbances are still poorly known. We investigated the responses of black bear, grey wolf, coyote, fisher, lynx, red fox, American red squirrel, white-tailed deer, moose, caribou, and snowshoe hare to both natural habitat and disturbance associated with anthropogenic features within Alberta's northeast boreal forest. We used a novel community-level modelling framework on three years of camera-trap data collected in an oil sands landscape. This framework allowed us to identify the natural and anthropogenic features which explained the most variation in occurrence frequency among functional groups, as well as compare responses to linear and non-linear anthropogenic disturbance. Occurrence frequency by predators was better explained by anthropogenic features than by natural habitat. Both linear and non-linear anthropogenic features helped explain occurrence frequency by prey and predators,

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although the effects differed in magnitude and spatial scale. To better conserve boreal biodiversity, management actions should extend beyond a focus on caribou and wolves and aim to restore habitat across a diversity of anthropogenic disturbances and monitor the dynamics of the entire mammal community.

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1. Introduction

Biodiversity has greatly declined in the Anthropocene (Dirzo et al., 2014), continues to decline despite increasing human response (Butchart et al., 2010), and is unlikely to stop declining in the future given expected trends in human consumption (Bellard et al., 2012). Anthropogenic landscape disturbance is a global driver of this biodiversity loss (Foley et al., 2005) due to its direct effects on habitat availability, quality, and connectivity (Fahrig, 2003). Although many studies have shown that anthropogenic disturbances are major drivers of biodiversity loss, the cumulative and interactive effects of the many forms of disturbances are still poorly known. A key limitation of many previous studies has been a narrow focus on single species, while broader understanding requires approaches that consider community-level responses to disturbance (Cavada et al., 2019; Zipkin et al., 2010).

Forest disturbance affects wildlife species in myriad ways, including spatial legacies relating to the composition and configuration of remaining forest (James et al., 2007). The effect of disturbance on wildlife depends on the character, extent, and intensity of the disturbance, as well as interactions among new disturbances and the legacies of previous disturbances (Côté et al., 2016). Individual and cumulative forest disturbances, and their consequent effects on habitat quality and availability, result in complex wildlife behavioral responses and altered community-level interactions (Courbin et al., 2014). Improved understanding of such mechanisms underlying biodiversity loss is needed to improve conservation decisions (Maxwell et al., 2016). Such decisions are made more difficult by increasing uncertainty when multiple species are threatened (Nicholson and Possingham, 2007), such as in hotspots of biodiversity and areas of intensive development.

Western Canada's oil sands region experiences disturbances from forestry and energy sector activities as well as municipal and transportation infrastructure, which interact to modify the landscape in ways without historical or global analogues (Pickell et al., 2015). These disturbances are also having significant effects on regional vegetation (Abib et al., 2019) and wildlife (Murdoch et al., 2020), especially mammal communities (Fisher and Burton, 2018). Notably, boreal woodland caribou (*Rangifer tarandus caribou*) populations, an ecotype of caribou, are declining across Canada partly due to industrial disturbance, and the species has consequently been listed as "Threatened" in the Species at Risk Act (Government of Canada, 2019). Caribou declines across its range have been driven by industrial development and consequent habitat loss, predation, and indirect processes such as apparent competition (Beauchesne et al., 2014; Boutin et al., 2012; Hebblewhite, 2017; Wasser et al., 2011).

Disturbance-mediated changes to the spatial structure of boreal forest landscapes have altered historical relationships between caribou, their predators, and other prey species. Predation of adult and neonate caribou by wolves (*Canis lupus*) (Latham et al., 2011b; McLoughlin et al., 2003) and of neonates by black bears (*Ursus americanus*) (Latham et al., 2011a) is thought to be the primary proximate cause of decline for caribou in the oil sands region of northeast Alberta, as well as in other parts of its range (Festa-Bianchet et al., 2011). Wolf numbers have increased, following increases in populations of white-tailed deer (*Odocoileus virginianus*), and possibly moose (*Alces alces americanus*) and beavers (*Castor canadensis*) (Latham et al., 2011c, 2013). This increase in prey has likely followed the landscape alteration associated with human development, through the increased ungulate forage provided by the conversion of mature forest into early seral vegetation

(Fisher and Wilkinson, 2005). The intensity of linear features use by wolf (Dickie et al., 2016) and white-tailed deer (Fisher et al., 2020) are strongly linked, and affected by both human use and obstacles created for attempts at restoration of linear features (Keim et al., 2019; Tattersall et al., 2020). Collectively, previous research suggests that cumulative effects of multiple, linear and non-linear, disturbances are effecting changes in community structure and predator-prey interactions (which most prominently, drive caribou population declines). However a community approach to mammal responses to widespread landscape change has only begun to be characterized (e.g. Bugar et al., 2018). Further community-level research is needed to advance our understanding of how community dynamics are changing within changing landscapes.

In this research, we address the knowledge gaps on community-level response to disturbance by: 1) comparing the effects of natural habitat vs. anthropogenic disturbance on predators, prey and the whole mammal community; 2) comparing the effects of linear vs. non-linear anthropogenic disturbances; 3) evaluating the influence of species interactions relative to habitat and disturbance. We suspect that simultaneous consideration of the responses of multiple interacting species may lead to different conservation recommendations than the current focus on only one or a few focal species, such as caribou and wolves.

Although several single-species studies have examined behavioral response to one type of anthropogenic feature – such as wolves moving faster down seismic lines (Dickie et al., 2016) – to date there has been no examination of responses to multiple anthropogenic disturbance types across the community. Are the effects of disturbance merely reflective of a single species' niche and confined to behavior, or are they consistent across multiple species, reflective of a species' functional role (e.g. predator vs prey), and do they scale up to occurrence frequency? This is the novel perspective of a community analysis approach seeking to find generalizable patterns across suites of mammal species. We hypothesized that anthropogenic features would influence predators to a greater extent than prey, given the documented heavy use of anthropogenic landscape features by wolves (Latham et al., 2011a; Lesmerises et al., 2012; McKenzie et al., 2012; Wasser et al., 2011) and the principle of trophic amplification (Kirby and Beaugrand, 2009). We also hypothesized that among anthropogenic features, linear features would predominate as the best-supported predictors of predators' occurrence frequency, given their apparently outsized influence in the single-species literature. Finally, we hypothesized that prey with the highest biomass in this system – snowshoe hares and white-tailed deer – would most influence predators' occurrence frequency.

To test these hypotheses, we measured the frequency of occurrence of caribou, moose, wolves, bears, and other species, relative to both natural habitat and disturbance associated with anthropogenic features within Alberta's northeast boreal forest. We use a novel community-based methodological framework based on count data from unmarked populations which enables us to explore how varying mammal habitat use, as measured by frequency of occurrence across space, is explained by different types of predictors in the landscape. More precisely, we partitioned the explanatory power (R^2) of community-level models of the occurrence frequency of 11 mammal species between best-supported natural and anthropogenic predictors. Building on the fractions of variation explained by different groups of predictors, we discuss how our study provides ecological insights beyond studies focused on a single species. Based on our findings, we stress the conservation value of

the complementary information brought by a community-level modelling approach to the boreal mammal community.

2. Materials and methods

2.1. Study area

Our study was conducted in the boreal forest northeast of Lac La Biche, Alberta, Canada (Fig. 1). The study area included the area around Christina Lake and Winefred Lake, north of the Cold Lake Air Weapons Range, and is approximately 3000 km². This mosaic-like forested landscape is mostly composed of white (*Picea glauca*) and black spruce (*Picea mariana*),

aspen (*Populus tremuloides*), jack pine (*Pinus banksiana*), and muskeg dominated by bog Labrador tea (*Rhododendron groenlandicum*). Anthropogenic disturbance is extensive with forestry and energy sector activities, including roads distributed over the study area (Fig. 1). Averaged over 1-km² cells within the study area, the percentage of seismic lines area per cell is 1.02[0.89] %, and the density of total disturbance area per cell is 2.72[3.27] %.

2.2. Faunal data

Mammal frequency of occurrence was sampled at 61 camera trap sites (Fig. 1). Reconyx PC900 Hyperfire™ infra-red remote digital

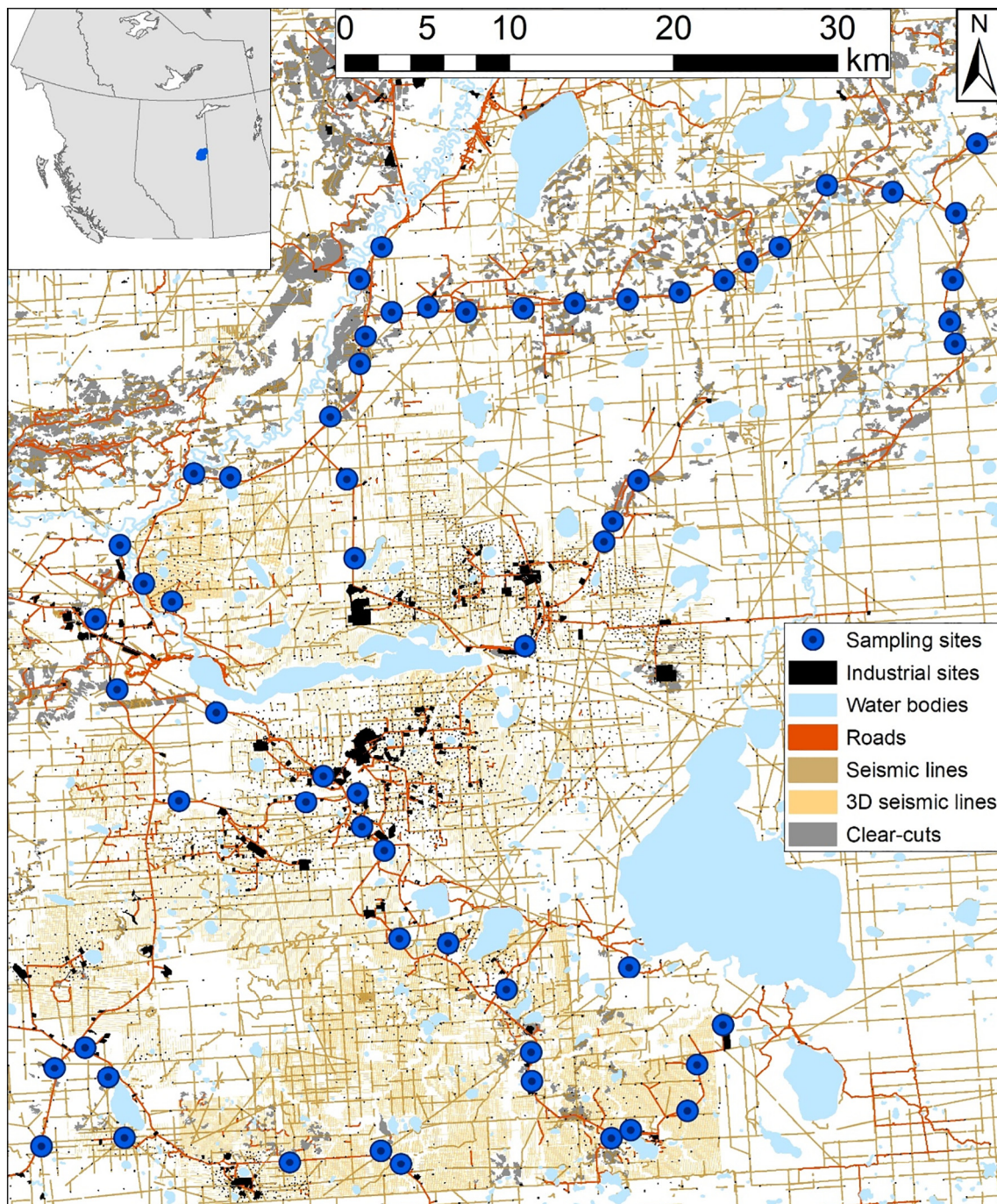


Fig. 1. The 61 camera-trap sites (dark blue circles) where mammal occurrence was surveyed in the northeast boreal forest near Winefred Lake, Alberta, Canada, between October 2011 and October 2014. Please note that the grid pattern associated with 3D seismic lines is at such a fine scale that individual lines resemble a fine mesh on our maps.

cameras (Holmen, WI, USA) were deployed for three years: October 2011–October 2014. The distribution of habitat types that are sampled within a landscape can greatly influence landscape-scale inferences (Dale and Fortin, 2014; Leroux et al., 2007). To increase the reliability of our extrapolations to other landscapes, and therefore have more general results, the camera traps were distributed across the landscape by using a constrained random stratified design intended to equalize representation of all habitat types. Camera locations were selected from among a set of 1-km resolution raster cells (our statistical units) covering the study area. We imposed a minimum 2-km distance between cameras to meet model assumptions of independence among statistical units (see Fisher and Burton, 2018 for more details). Among all 1-km² cells from the 3000 km² study area, 406 cells were identified as being reliably accessible; 61 final candidate cells were selected randomly within several forest strata (see *Environmental Data*). Cells that had no access were dropped and replaced from this pool. This had the effect that roads and trails were more highly represented within 250-m radius of sampling sites than proportional in the landscape. However, because these linear features were so ubiquitous in this landscape (Fig. 1), this effect disappeared beyond this distance, wherein linear features were represented in our sample proportional to the landscape.

Within grid cells, cameras were systematically deployed on active wildlife trails, that is trails with evidence of recent and substantial wildlife travel, at a minimum distance of 200-m from roads and human trails, including the ones used to access the camera trapping sites. Each trail was independent from others in adjacent cells. The mean and median distances between sampling sites were 33.1 [17.3] km and 32.2 km, respectively. The resulting design captured the range of this landscape's anthropogenic footprint and natural heterogeneity. We obtained permission from government land officers and industry leaseholders to access all sampling areas. Camera traps were neither lured nor baited. The camera trap survey had a total sampling effort of 60,937 camera trap-days which yielded 164,519 photographs, providing 141,140 images of mammal species. Among those 141,140 images, 134,482 were identified to species: black bears (2657 images), grey wolves (2508 images), coyotes (*Canis latrans*; 2290 images), fishers (*Pekania pennanti*; 326 images), lynx (*Lynx canadensis*; 1940 images), red fox (*Vulpes vulpes*; 197 images), American red squirrel (*Tamiasciurus hudsonicus*; 491 images), white-tailed deer (112,648 images), moose (500 images), caribou (273 images), and snowshoe hare (*Lepus americanus*; 10,652 images). The final dataset therefore included six predator species and five prey species.

To track responses of these mammals to landscape features, we used an index of occurrence frequency based on a minimum interval of 1 h between consecutive detection events of the same species at the same site. Such corrected occurrence frequency indices are commonly used in camera trap studies (Burton et al., 2015; Keim et al., 2019; Steenweg et al., 2017; Tattersall et al., 2020). Occurrence frequency metrics from camera trap surveys incorporate both the number of individuals at a site and the repeated use of a site by an individual(s), which is mediated by movement behavior (Stewart et al., 2018). We temporally truncated data to avoid the problem of curious, lingering species such as bears being over-represented in the occurrence frequency metric because they take time to investigate the camera, whereas deer and other species do not. The choice of 1 h was also guided by an assessment of the maximum time a camera-exploration behavior occurred in our dataset. We further consider this metric to be reliable as recent simulation-based work has shown a close relationship between abundance and detection rates for multiple species with varying home range sizes and movement behavior (Broadley et al., 2019). Image capture of groups of animals were recorded as a single occurrence. Herein we study co-occurrences, which we conceptually link to the potential for trophic interactions (e.g., predator and prey). As the field settings were the same for all cameras and because we do not compare occurrence frequency across species, we avoided introducing a systematic bias in our analysis through camera placement.

We standardized for sampling effort by dividing the number of detections by the number of camera days at each site. Camera sampled for an average of 997.44 [152.88] days. The resulting site \times species matrix of occurrence frequency was standardized using a Hellinger-transformation prior to analysis, which is a common way to improve the statistical properties of RDA models, while respecting the role of rare species (Legendre and De Cáceres, 2013; Legendre and Gallagher, 2001; Peres-Neto et al., 2006).

2.3. Environmental data

We quantified natural landscape composition using the Alberta Vegetation Inventory (AVI), a digital, vector format, species-level forest inventory dataset provided by Government of Alberta (Table 1). These data were reclassified into two broad categories. We classified black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), white spruce (*Picea glauca*), and balsam fir (*Abies balsamea*) as “coniferous”. Paper birch (*Betula papyrifera*), aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*) and tamarack (*Larix laricina*) were classified as “deciduous”. Within each 1-km² raster cell, we extracted the area of each AVI polygon along with the dominant canopy species in the polygon and multiplied that by the percentage of the canopy in that polygon. We classified each polygon as lowland if the moisture regime was recorded as aquatic or wet, or upland if it was not. The canopy cover designations and moisture regime information were combined to create thirteen land cover categories (Table 1). We calculated the area (m²) of each habitat category around each sampling site at different scales: we used 20 radii from 250 m to 5000 m, in 250 m increments. Those scales have previously been shown to be meaningful for the boreal forest mammal community (Fisher et al., 2011).

We also calculated the area (m²) of each anthropogenic feature around each sampling site (Table 1), using the Alberta Biodiversity Monitoring Institute Human Footprint Map Version 1.1 (ABMI, 2019). As low-impact seismic lines were not sufficiently captured in the ABMI (2019) dataset, we used buffered linear features data from 2012 ABMI, (2019) to supplement the ABMI (2019) data (Table 1). We calculated the percentage of area occupied by linear features (buffered to create polygons from polylines) around each sampling site. Similar linear features open data is now also available through open governmental websites (Government of Alberta, 2019).

2.4. Creation of multi-scale spatial variables

Spatial autocorrelation in ecological data can confound efforts to characterize the effect of the environment on community structure (Dale and Fortin, 2014). Such autocorrelation can be included and controlled for in statistical models of ecological variation through the use of synthetic spatial variables such as Moran's eigenvector maps (MEM) (Borcard et al., 2004; Borcard and Legendre, 2002; Dray et al., 2006; Legendre and Legendre, 2012). MEMs are computed as the eigenvectors of a spatial weighting matrix based on a set of geographical coordinates (i.e., sample sites). We used the *dbmem()* function from the *adespatial* R (R Core Team, 2019) package (Dray et al., 2019) to create the MEMs. MEM analysis is a multi-scale spatial analysis that produces uncorrelated spatial Eigen functions, which we can be used to identify spatial patterns of variation in the response variable(s) across a range of spatial scales. The first few MEM variables created through the algorithm (large Moran's I coefficients) represent broad-scale processes. MEM variables with smaller Moran's I coefficients represent fine spatial autocorrelation generated by local processes (Supp. Fig. 1). MEMs can represent either positive or negative spatial autocorrelation.

2.5. Regression framework

We used redundancy analysis (RDA; Legendre and Legendre, 2012) to model the association between occurrence frequency of mammal

Table 1

Description and classification of natural and anthropogenic data extracted in our study area and used in the selection process.

Habitat or feature class	Source	Description
Upland deciduous	AVI	(Aw, Pb, Bw \geq 70% canopy), moisture = d or m ^{a,b}
Lowland deciduous	AVI	(Aw, Pb, Bw \geq 70% canopy), moisture = w or a
Upland mixedwood	AVI	(40% -60%) canopy, moisture = d or m
Lowland mixedwood	AVI	(40% -60%) canopy, moisture = w or a
Upland spruce	AVI	(Sb, Sw, Fb \geq 70% canopy), moisture = d or m
Lowland spruce	AVI	(Sb, Sw, Fb \geq 70% canopy), moisture = w or a
Pine	AVI	All Pj (\geq 70%)
Tamarack	AVI	All Lt (\geq 70%)
Open wetland	AVI	<6% crown closure; moisture = w or a
Upland shrubs	AVI	>25% shrub cover; <6% tree cover; moisture = d or m
Water	AVI	Standing or flowing water
Nonforest	AVI	Areas with <6% canopy
Cutblock	ABMI	Forest harvested cutblocks of any age
Block feature	ABMI	Combination variable including mining borrow pits, dugouts, sumps, industrial sites, and sites categorized as "other disturbed vegetation". No mature trees.
Well site	ABMI	Energy sector sites including a well and surrounding area, usually grassy vegetation
3D seismic line	UALF	3D seismic energy sector exploration lines, deployed in a high-density hashmark pattern. ^c
Cutline	UALF	Traditional, single energy sector exploration lines, less dense than 3D seismic lines.
Roads (all)	UALF	Combination variable of one- and two-lane roads, gravel and paved, and unimproved roads.
Trails (all)	UALF	Combination of trails and truck trails.
Driveway	UALF	
Electrical transmission line	UALF	
One-lane gravel road	UALF	
One-lane paved road	UALF	
Pipeline	UALF	Energy sector pipelines and their rights of way, usually wide and grass-covered.
Rail	UALF	
Trail	UALF	Trails navigable by off road vehicles, horses, and people but not trucks.
Truck trail	UALF	Trails navigable by trucks but without gravel.
Two-lane gravel road	UALF	
Two-lanes paved road	UALF	
Unimproved road	UALF	
Borrow/Pit/Dugout/Sump	ABMI	
Industrial site	ABMI	
Other disturbed vegetation	ABMI	
Rail (hard surface)	UALF	
Rail (vegetated verge)	UALF	
Road (hard surface)	UALF	
Road (vegetated verge)	UALF	
Road/Trail (vegetated verge)	UALF	
Seismic line	UALF	

^a AVI = Alberta Vegetation Index; UALF = University of Alberta Linear Features Map Updated 2012; ABMI = Alberta Biodiversity Monitoring Institute Human Footprint Map Updated 2010.

^b Aw = aspen, Pb = poplar, Bw = white birch, Sb = black spruce, Sw = white spruce, Fb = balsam fir, Pj = jack pine, Lt = tamarack/larch; d = dry, m = mesic, w = wet, a = aquatic.

^c Linear features were buffered for areal calculations as follows: 'Two Lane Undivided Paved Road': 9 m; 'One Lane Undivided Paved Road': 6 m; 'Rail Line': 5.5 m; 'Rail Line-spur': 5.5 m; 'Two Lane Gravel Road': 7 m; 'One Lane Gravel Road': 5 m; 'Driveway': 2 m; 'Unimproved Road': 6 m; 'Trail': 6 m; 'Truck Trail': 6 m; 'Electrical Transmission Line': 17 m; 'Pipeline': 12 m; '3D': 2 m; 'Cutline': 2 m.

species and groups of environmental and spatial predictors. We used the *rda()* function from the *vegan* R package (Oksanen et al., 2018) to perform the RDAs. Groups of predictors (submodels) were used to model hypothesized forces driving mammal abundance, including: spatial autocorrelation (MEMs), anthropogenic disturbance, natural

habitat, and predation, when relevant. The response term of the models was multivariate and included the occurrence frequency of several species at once, and therefore did not consist of one variable with occurrence frequency of different species lumped together. We chose a community-level approach because it explicitly addresses processes creating co-occurrence patterns beyond shared abiotic requirements of species, such as biotic interactions (Baselga and Araújo, 2009; Maguire et al., 2016). Additionally, community-level models have been shown to be at least similar to an assemblage of single-species models in predicting species distributions, with significant improvement for rare species (Hui et al., 2013; Maguire et al., 2016).

We used a two-step approach to narrow down the relevant predictors for each analysis: 1) selection of the best scales for each environmental predictor and 2) selection of the best environmental predictors overall. First, we used a modified forward selection procedure (Blanchet et al., 2008) to select the best scale(s) for each environmental predictor. We used the *forward.sel()* function from the *adespatial* R package (Dray et al., 2019) with a alpha threshold of 0.1, instead of the threshold of 0.05 used in the rest of our analyses, to be more liberal during this first step. A potential pitfall associated with the use of forward selection to select environmental predictors is the overestimation of the amount of explained variance (Diehr and Hoflin, 1974). The modified two-step forward selection we used avoids overestimating the coefficient of multiple determination by conducting a global test of significance prior to using two stop criteria (Blanchet et al., 2008). We tested the significance of the joint effect of the pre-selected variables on response variables within each sub-model independently using an ANOVA-like permutation test (Legendre and Legendre, 2012). We tested the global significance separately for negative and positive spatial eigenvectors to provide enough degrees of freedom (Blanchet et al., 2008) and therefore applied Sidak's correction to the alpha level of rejection of the null hypothesis (Sidak, 1967) in order to have an appropriate rejection rate overall.

Second, if a sub-model was deemed significant in the previous step, we used the same forward selection procedure used in the first step to select the best variables to keep in a final model. When using MEM among the spatial predictors, we tested and forward selected separately for each species and used the union of all selected predictors (Peres-Neto and Legendre, 2010).

Finally, we applied variation partitioning to our selected multivariate model of mammal occurrence frequency. Using this approach we sought to quantify the unique and shared contributions of each retained predictor to the variation of community composition data (Borcard and Legendre, 1994; Peres-Neto et al., 2006). Specifically, we assessed the unique and shared contributions of the following categories of predictors: 1) Natural habitat, 2) Anthropogenic features, 3) Spatial autocorrelation, and 4) Occurrence frequency of predators or prey when relevant. Variance partitioning was implemented using the *varpart()* function in the *vegan* R package (Oksanen et al., 2018) to perform the variation partitioning. Therefore, the intersecting fractions of the variation explained by two (or more) submodels describe the variation that is not distinguishably explained by one of them and do not describe the effect of interactions between submodels. We also used variation partitioning on the following submodels: 1) Linear anthropogenic features, and 2) Non-linear anthropogenic features in a subsequent analysis.

3. Results

3.1. Performance of models and submodels

The frequency of occurrence of the mammal community across this highly disturbed landscape was shaped by a combination of anthropogenic features, natural habitat, spatial autocorrelation, and predation,

as all four of these submodels were consistently significant in explaining variation in the observed occurrence frequency of mammals (Table 2).

As hypothesized, the anthropogenic features submodel explained most (30% with a total of 37% with a full model) of the variation in the occurrence frequency of predators. On the other hand, the natural habitat submodel explained most (43% with a total of 51% with a full model) of the variation in the occurrence frequency of prey (Table 2). The natural habitat submodel also explained most of the variation at the whole community level, that is when considering all species in the dataset.

Although the anthropogenic features submodel was the best submodel for predators, it explained about the same amount of variation in both predators (30%) and prey (27%) (Table 2). Although significant, the spatial submodel explained the least variation in all three (predators, prey and whole community) analyses (Table 2) and most of the variation explained by the spatial submodel was consistently shared with at least one other submodel (Fig. 2). This is expected as natural and anthropogenic predictors were themselves spatially-structured, at a scale close to one of the scales covered by MEM. Using a functional group (prey or predators) as a submodel consistently explained more than 10% of the variation in occurrence frequency (Table 2).

Pure fractions of explained variation –those that were unique to submodels– were consistently smaller than the sum of shared/common fractions within a submodel (Fig. 2). In ecological terms, this means that for example, natural habitat and anthropogenic features—which are two different submodels—jointly explain mammal occurrence frequency. That is their respective explanatory power to describe mammal occurrence frequency intersect substantially (Legendre and Legendre, 2012). High shared fractions also mean that only a limited part of the variation in occurrence frequency is explained by only one of the submodels. However, the best submodel for prey (natural habitat), predators (anthropogenic features), and the whole community (natural

habitat) consistently had substantial pure fractions (Fig. 2). General qualitative conclusions were not meaningfully affected by changing the temporal bin size (1-hour delay) of our index.

3.2. Most important environmental variables and canonical axes

Anthropogenic features selected as important –whether for predators, prey or the whole community – included a diversity of linear features (3D seismic lines, roads, and trails), as well as polygonal disturbance features (Table 2). Upland deciduous habitat was the only habitat identified as important across functional groups, although lowland mixed forest habitat, open wetland and lowland spruce were also selected by prey or predators (Table 2). Snowshoe hare was the only prey species selected as a significant predictor of predator occurrence frequency (Table 2). This finding only partially supports our hypothesis. The occurrence frequency of lynx and coyote best explained the occurrence frequency of prey, which we had not hypothesized based on the literature (Table 2). The vast majority of the explained variation is concentrated on the first axis for prey (Supp. Table 2) and the whole community (Supp. Table 3) with respectively 95% and 87% of the explained variation explained by the first RDA axis, compared with 50% for predators. Coyotes and lynx have the highest fit among predators in the whole community analysis (Supp. Table 3) which parallels their selection as predictors for prey occurrence frequency (Table 2). In Supp. Table 1, wolf occurrence frequency is not explained by the same canonical axis (RDA 2) as black bear or coyote occurrence frequency (RDA 1), with RDA 1 explaining more variation than RDA 2. Triplot visualizations of the RDA results also highlight the differences between species and their relationships with the environmental variables selected previously (Supp. Fig. 2).

3.3. Spatial scale

Natural habitat influenced the occurrence frequency of prey at smaller spatial scales than that of predators, as all selected variables were best supported at scales under 1-km for the occurrence frequency of prey, whereas there was no selected variable with a scale below 1.5 km for the occurrence frequency of predators, with one variable selected at the largest scale available (5 km). Linear and block anthropogenic features which were selected for the occurrence frequency of predators were supported from smaller to larger scales, whereas anthropogenic features were consistently selected for the occurrence frequency of prey at smaller scales (Table 2).

The same pattern was supported by the selected variables in the spatial submodel. Indeed, broader scale MEMs (e.g. MEM 2 which may represent landscape-wide variation) and intermediate scale MEMs (e.g. MEM 6 which may represent more local between-site variation) were selected for predators, while the only MEM selected for prey (MEM 8) was a smaller scale MEM (Table 2).

3.4. Linear vs. block features

Within the anthropogenic features submodel, the relative importance of linear and nonlinear features varied across prey and predators and as hypothesized, linear features seemed to be more important than block features in explaining predator occurrence frequency (Table 3). Indeed, linear features explained twice as much variation as polygonal features do for predators, while both types of anthropogenic features explained around the same amount of variation for prey (Table 3). Moreover, in contrast to the analyses using the natural habitat, spatial and predation submodels, there was very little shared explained variation among linear and block features, with most of the explained variation being in the pure fractions.

Table 2

Adjusted coefficients of determination for each submodel, along with the selected variables, for each functional group. Number in parentheses indicate scale of selected variables in kilometres. Variables selected across functional groups are in bold.

Functional group		
Predators	Prey	Whole community
Submodel		
<i>Natural habitat</i>		
0.17	0.43	0.33
Upland deciduous (1.75)	Upland deciduous (0.75)	Upland deciduous (0.75)
Lowland mixed (5)	Lowland spruce (0.25)	Lowland spruce (0.25)
Lowland mixed (1.75)	Open wetland (0.25)	Open wetland (0.25)
<i>Anthropogenic features</i>		
0.3	0.27	0.22
Block feature (0.5)	Block feature (1)	Block feature (1)
3D seismic line (0.5)	3D seismic line (0.25)	3D seismic line (0.25)
Road/Trail (veg.) (1.5)	Road/Trail (veg.) (1.5)	Road/Trail (veg.) (1.5)
Industrial site (4)		
Industrial site (5)		
Road (veg.) (4.75)		
Trails (all) (2.5)		
	Cut block (0.25)	Cut block (0.25)
<i>Spatial variables</i>		
0.14	0.07	0.04
Longitude		
MEM 2		
MEM 3		
MEM 6	MEM 8	MEM 8
<i>Other functional group</i>		
0.1	0.2	not applicable
Snowshoe hare	Coyote	
	Lynx	
<i>All submodels</i>		
0.37	0.51	0.39

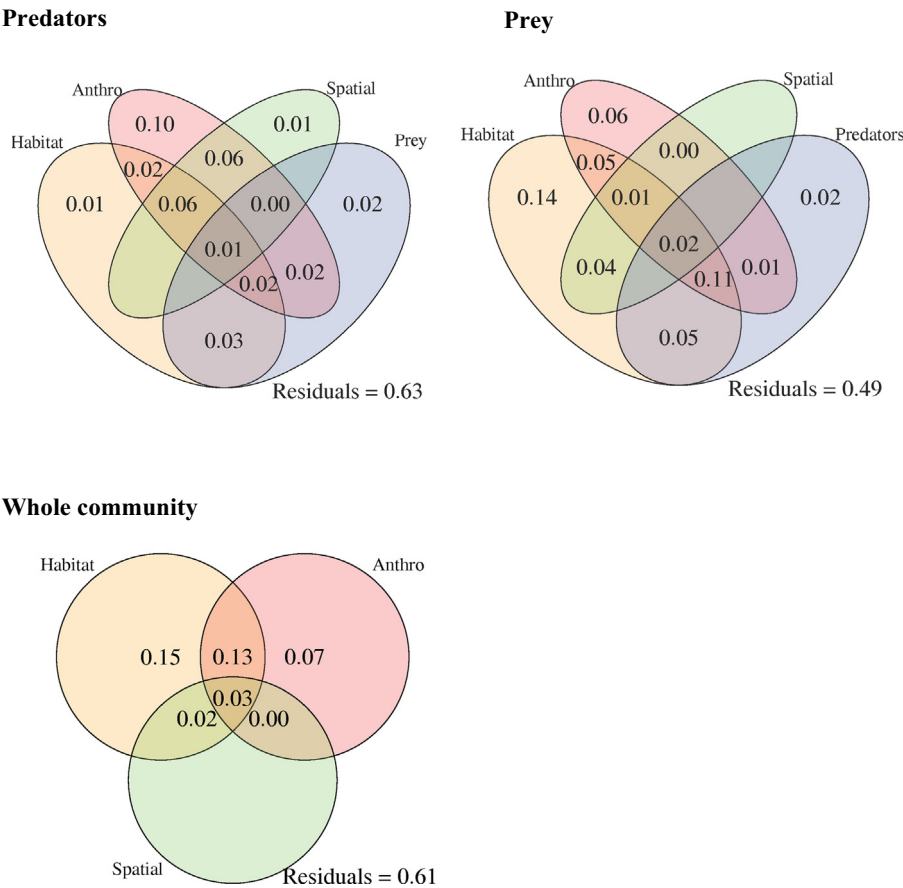


Fig. 2. Partition of the variation of the occurrence frequency of predators, prey and the whole community, among the explanatory submodels. Fractions of the explained variation are expressed in adjusted coefficient of determination. Intersections represent parts of the variation which prediction is shared by different submodels. “Habitat” refers to natural habitat and “Anthro” refers to anthropogenic disturbances. Values less than or equal to 0 are not shown.

4. Discussion

4.1. Impacts of anthropogenic features on the boreal mammal community

Anthropogenic landscape disturbance has a major influence on the boreal oil sands mammal community. We found that the anthropogenic disturbances such as cut blocks and linear features such as 3D seismic lines, roads, and trails influenced both predator and prey communities (Table 2). These features had a greater effect on predators than prey to the extent that anthropogenic legacies were found to have a greater effect on predator occurrence frequency than natural habitat variation. The variance explained by anthropogenic features was distinct from that explained by natural habitat for predators. We also found that anthropogenic features affect predators at larger spatial scales than for prey (Table 2). Our findings greatly elaborate the relationships between anthropogenic disturbance and mammal occurrence frequency (Fisher and Burton, 2018; Toews et al., 2017, 2018), and further contribute to our understanding of how the persisting spatial legacies of industrial

forestry and the energy sector affect different components of the boreal mammal community.

The mechanism by which human disturbance affects mammal communities is the conversion of intact mature forest to early seral stages, changing both resource availability and animal movement. Early seral vegetation in young cutblocks is preferred by moose (Cederlund and Okarma, 1988; Rempel et al., 1997). Clearcutting can produce spatial legacies similar to those created by wildfire in terms of spatial extent and successional responses which results in an increase in available forage in the years following disturbance (Crête et al., 1995; Krefting, 1974). The early seral vegetation present in cutblocks is also beneficial for white-tailed deer (Fisher et al., 2016; Fisher and Wilkinson, 2005; St-Louis et al., 2000). Block features (e.g., clear cuts) were identified as important for predators, which is not surprising given their higher abundance of anthropophilic and early-seral-dependent prey such as white-tailed deer (Fisher et al., 2020; Fisher and Burton, 2018). Our results are also consistent with the hypothesis that linear features facilitate predators including coyotes (Boisjoly et al., 2009) and wolves (Dickie et al., 2016; McKenzie et al., 2012; Whittington et al., 2011). Whether the associations we highlighted are behavioral, numerical (and associated with resource competition, apparent competition, or human-driven increased mortality), or both requires further study.

Considering the nature of the verges of roads and trails is relevant to understanding their effects on the boreal mammal community. By using many variables related to roads and trails in the selection process (Table 1) instead of grouping them a priori, we allowed the explicit modelling of roads and trails with vegetated verges (Table 1). Our results suggest that potentially negative effects of roads and trails associated with direct mortality or risk avoidance may be offset by the presence of vegetated verges on the sides of those linear features

Table 3
Variation partitioning of occurrence frequencies among linear and block features, within the Anthropogenic features submodel. Pure and shared fractions of the explained variation are displayed.

Feature type	Functional group	
	Predators	Prey
Linear (pure)	0.2	0.12
Shared	0.01	0.02
Block (pure)	0.09	0.13

which provide forage subsidy. Roadside forage subsidy has been reported to be attractive to white-tailed deer (Bellis and Graves, 1971). Furthermore, telemetry studies have suggested such a mechanism is possible for white-tailed deer (Darlington, 2018).

Although anthropogenic disturbance explained about the same amount of variation in prey and predator communities, this variation differed in its influence relative to natural habitat. More than 70% of variation in prey occurrence explained by anthropogenic features was shared with natural habitat (Fig. 2); this means variation in mammal occurrence frequency can be explained by either. The fact that anthropogenic features shared such a large part of the variance they explain with that of natural habitat might be a clue that the effect of anthropogenic features on prey is more dependent on the type and/or density of surrounding natural habitats than for predators. Indeed, mammals, and prey in particular, require a diversity of boreal forest habitats to live and may conditionally avoid certain natural and altered habitats. For example, moose require mature forest for cover (Forbes and Theberge, 1993; Herfindal et al., 2009; Månsson et al., 2007) and its availability could supersede any positive effects of forage subsidy from vegetated linear features or industrial sites. Smaller prey (e.g., snowshoe hare, red squirrel) are known to avoid recent clearcuts (Fisher and Wilkinson, 2005; Lewis et al., 2011; Newbury and Simon, 2005) and linear features (Bakker and Van Vuren, 2004; Fisher and Wilkinson, 2005; Oxley et al., 1974). This appears to be a major difference between prey and predators in our study area, where only about 33% of the explained variation in predator abundances was shared between anthropogenic features and natural habitat. However, further research is needed to identify which parts of the natural landscape interact with anthropogenic features. If interactions are indeed responsible for the patterns of shared variation in our data, then an increase of the density of anthropogenic features could change the dynamics of predators more independently of surrounding natural habitat than for prey.

Both anthropogenic features and spatial structure (i.e., MEMs) were selected at small scales by prey. This suggests that when linear and block features are physically proximal, their effect on prey is strongest. A heavily disturbed landscape would mean that strong but small-scale effects on prey are nonetheless widespread. Because predators are affected by environmental processes at larger scales (i.e., farther away), and because predation plays a major role in prey distribution and hence community composition, the effect of anthropogenic features on predators may also translate on prey and vice versa (Wisze et al., 2013).

4.2. Linear vs. block features

Both linear and block features influence mammal occurrence frequency in the boreal forest, although their effects differed between predator and prey species. As hypothesized linear features were more important than block features in explaining predator occurrence (Table 3). Nonetheless, block features still explained about 10% of the variation in predator occurrence. Those 10% represent 25% of the total variation explained by the full model. Block and linear features explained about the same amount of variation in prey species. These contrasting results illustrate the importance of how the shape of human disturbance (linear vs. block) affects mammal communities – a basic tenet of landscape ecology but often neglected in management. Previous studies have shown the importance of block features for specific boreal species, such as the avoidance of clearcuts by caribou (Lafontaine et al., 2019; Sorensen et al., 2008). Other studies compared both linear and block features on specific species (e.g. Houle et al., 2010; Beauchesne et al., 2013), however, to our knowledge, this is the first study that explicitly compared the two types of features from a community perspective.

A surprising outcome of partitioning variation explained by linear vs. block features was that each explained different parts of the variation in occurrence frequency, in both prey and predators. Most of the explained

variation is present in pure fractions (Fig. 2); linear features and block features affect the whole mammal community in measurably different ways. The low shared fraction does not mean there is no interaction between these feature types, but that they explained very different parts of the variation in mammal occurrence frequency (Legendre and Legendre, 2012). Focusing only on linear features as an ecological mechanism yields only part of the answer; and setting only linear features as a target for conservation will solve only a part of the problem.

4.3. A fuller picture of the community dynamics

While a large amount of research has focused on wolves and black bears as the main predators in this community, lynx and coyotes are also important components. Indeed, their occurrence frequency significantly influenced the occurrence frequency of prey (Table 2). This could be expected given their high densities in boreal oil sands landscapes (Burgar et al., 2018). Coyotes are adaptable to disturbance and have been expanding their range for several centuries (Levy, 2012) and they can markedly affect mammal communities (Heim et al., 2017). Large prey (e.g., deer) tend to represent the majority of coyote diet in eastern Quebec (Boisjoly et al., 2009). Large coyotes have successfully preyed on moose (Benson and Patterson, 2013) and caribou calves (Crête and Desrosiers, 1995; Latham et al., 2013) with a detrimental effect on recruitment (Frenette et al., 2020; Lewis et al., 2017). Wolves have weaker environmental associations than coyotes (Supp. Tables 1 and 3, and Supp. Fig. 2). This does not mean that wolves are not influenced by the landscape, but perhaps suggests that the frequency of occurrence of wolves could change less with further anthropogenic perturbation of the landscape than that of coyotes. Futureproofing conservation decisions will require consideration of coyote's responses to disturbance, as well as wolves'.

4.4. Study limitations and further research

Choosing adequate indices of occurrence frequency/relative abundance, or other demographic metrics, from unmarked data, such as most camera trap data, is challenging (Burton et al., 2015; Chandler and Royle, 2013; Dénes et al., 2015). Here we assumed that zeros observations were true zeroes, rather than detection error, which we limited by avoiding obstructions, limiting false triggers, and optimizing wildlife detection, but we recognize that habitat structure and animal movement both influence detection. Thoroughly validating the interpretation of occurrence frequency/relative abundance indices as proxies of true abundance, or other demographic properties, involves testing assumptions about the functional relationship between the demographic property under study and those indices. Indeed, many assumptions behind the metrics based on camera trap data remain untested (and sometimes untestable) in many empirical studies. We made no assumption about the shape of the relationship between our index and actual true abundance as we cannot know whether the index is driven by changes in local abundance vs. behavior. Towards the goal of picking an accurate index and validate its use, we highlight the importance of simulations including species interactions and variation in occurrence frequency, in testing different indices of occurrence frequency. Recent advances in using simulations to guide use of camera trap data (Broadley et al., 2019; Burton et al., 2015; Hofmeester et al., 2017) are promising.

We conducted our study in a large, heavily developed boreal landscape that is typical of areas actively exploited by forestry and oil and gas development. As such, our findings do not necessarily apply in less-impacted regions of the boreal forest. In investigating such as large area it is difficult to provide fine-scale sampling resolution; indeed, this is a trade-off with large-scale mensurative studies, and there is no evidence to suggest the resolution of our data affected conclusions. Variables selected for the whole community were the same as variables selected for prey which may be associated with the dominance of prey, especially white-tailed deer, in driving community-level associations

in this dataset. The relationship between the area of habitat that best predicts boreal mammal species occurrence is not scaled 1:1 with body size (Fisher et al., 2011), and the signals we detected suggested the data captured at this resolution observed a breadth of processes fitting most species. We plan to, and encourage other research groups to, replicate our study in other boreal landscapes, notably those with different amount of anthropogenic footprint. Future work in this regard will focus on deploying higher densities of camera-trap stations to better capture differences in home range sizes among species. Finally, information-theoretic approaches provide a powerful way to rank candidate models and test hypotheses (Stephens et al., 2005) and a comparison of their application with our results could help us to better discern the assumptions of our analyses.

4.5. Applying ecological complexities to managing the boreal forest mammal community

Most of the variation explained by the anthropogenic features submodel is shared with the natural habitat submodel. This, and the fact that natural habitat is the most important prey submodel, could hint that we should generally consider natural habitat as the most limiting factor for prey. However, we showed that a variety of anthropogenic features shape the distribution of predators and prey, which suggests that conservation activities focused on areas of undisturbed habitat (such as protected areas strategies) may not adequately address the relevant ecosystem dynamics necessary to conserve the mammal community. Moreover, the large scale at which some anthropogenic variables were selected for predators, suggest that there might unfortunately be very few areas in our study area without a direct or indirect effect from linear or block features. We acknowledge that anthropogenic features may affect the mammal community at larger spatial scales than we considered in this study area.

Both linear and block features influence patterns of the mammal occurrence frequency. Although the effects of block features on species within the boreal mammal community have been researched (Courbin et al., 2009; Courtois et al., 2007; Smith et al., 2000), linear features have been the main focus of recent boreal mammal conservation studies (DeMars and Boutin, 2017; Dickie et al., 2016; Latham et al., 2011b; McKenzie et al., 2012; Whittington et al., 2011). Because we found that block and linear features affect predators and prey in different unique ways, mitigation efforts should focus on reclaiming both types of features, to avoid favoring one group of species over another, and to ensure that trophic interaction networks remain intact. While we provide a general overview of how the environment, natural or anthropogenic, influences mammal community variation in human affected landscapes, further opportunities exist to refine this understanding and to improve seasonal and local management recommendations.

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CRedit authorship contribution statement

Julian Wittische: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization, Project administration, Funding acquisition. **Scott Heckbert:** Conceptualization, Writing - original draft, Writing - review & editing, Supervision, Project administration, Funding acquisition. **Patrick M.A. James:** Resources, Writing - review &

editing, Supervision, Project administration, Funding acquisition. **A. Cole Burton:** Conceptualization, Investigation, Data curation, Writing - original draft, Writing - review & editing, Supervision, Project administration, Funding acquisition. **Jason T. Fisher:** Conceptualization, Investigation, Data curation, Writing - original draft, Writing - review & editing, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2020.142500>.

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