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# Syntopic species interact with large boreal mammals' response to anthropogenic landscape change

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HIGHLIGHTS

- Mammals' response to anthropogenic landscape change depends on co-occurring species.
- Prey response to disturbance is exacerbated by co-occurring predators, and *vice versa*.
- Landscape disturbance and syntopic species operate synergistically for many mammals.
- Consequences of landscape change are contextual with the biotic community.

GRAPHICAL ABSTRACT
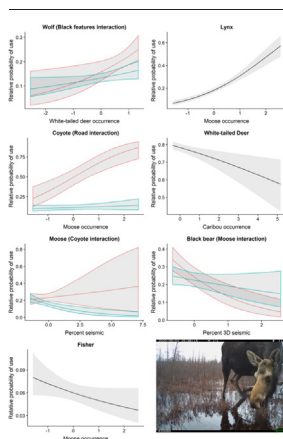
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ABSTRACT

Landscape change alters species' distributions, and understanding these changes is a key ecological and conservation goal. Species-habitat relationships are often modelled in the absence of syntopic species, but niche theory and emerging empirical research suggests heterospecifics should entrain (and statistically explain) variability in distribution, perhaps synergistically by interacting with landscape features.

We examined the effects of syntopic species in boreal mammals' relationship to landscape change, using three years of camera-trap data in the western Nearctic boreal forest. Using an information-theoretic framework, we weighed evidence for additive and interactive variables measuring heterospecifics' co-occurrence in species distribution models built on natural and anthropogenic landscape features. We competed multiple hypotheses about the roles of natural features, anthropogenic features, predators, competitors, and species-habitat interaction terms in explaining relative abundance of carnivores, herbivores, and omnivores/scavengers.

For most species, models including heterospecifics explained occurrence frequency better than landscape features alone. Dominant predator (wolf) occurrence was best explained by prey, while prey species were explained by apparent competitors and subdominant predators. Evidence for interactions between landscape features and heterospecifics was strong for coyotes and wolves but variable for other species.

Boreal mammals' spatial distribution is a function of heterospecific co-occurrence as well as landscape features, with synergistic effects observed for most species. Understanding species' responses to anthropogenic landscape change thus requires a multi-taxa approach that incorporates interspecific relationships, enabling better inference into underlying processes from observed patterns.

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1. Introduction

Landscapes are complex mosaics of resources and costs for mammal species. The shape and composition of the features, or patches, in a landscape mediate how a species exploits available resources (Dunning et al., 1992), while syntopic species – predators and competitors occurring at the same place and time as the focal species – add cost *via* direct mortality or competition for resource acquisition. This additive role of syntopic heterospecifics in altering a species' relationship to resources is the core of realized niche theory (Colwell and Rangel, 2009; Hutchinson, 1957). Together, landscape complexity layered with risk from heterospecifics creates a variably competitive spatial environment where species' behavioural responses (Basille et al., 2015; Creel et al., 2008) and population outcomes (Amarasekare, 2003; Chesson, 2000) are expected to vary markedly across space. Recent empirical evidence from multiple terrestrial systems (Fisher et al., 2013; Godsoe and Harmon, 2012; Sévêque et al., 2020) suggests syntopic heterospecifics explain additional variance in species distribution, beyond that attributable to resource availability. Thus species co-occurrences may also complicate a species' response to changes in resource availability incurred *via* anthropogenic landscape change.

As anthropogenic resource exploitation expands in space and time, biodiversity decreases, so understanding the mechanisms driving species' losses is critical to effective conservation decisions (Dirzo et al., 2014; Johnson et al., 2017; Maxwell et al., 2016). Modelling species' relative abundance in relation to both species co-occurrence and anthropogenic disturbance helps to identify underlying mechanisms of biodiversity loss. Although syntopic co-occurrence does not *de facto* signal species interactions (Blanchet et al., 2020; Peterson et al., 2020), syntopy is necessary for those interactions to occur, so serves an indicator of potential interactions. We asked whether the relative abundance of a species' co-occurring predators, prey, competitors, and apparent competitors (Holt, 1977; Holt and Kotler, 1987) further explain species' relationship to anthropogenic landscape change. We asked whether the effects of heterospecifics are additive, or synergistic: influencing the relationship between a mammal and landscape features, as evidenced by a statistical interaction term.

We explored these questions in one of the most rapidly changing regions of North America, the western boreal forest: a useful model for this test as the timber, mining, and petroleum resources which contribute substantially to global economies (Bayoumi and Mhleisen, 2006; Schindler and Lee, 2010; Venier et al., 2014) have altered landscapes outside the range of contemporary or historical natural variability (Pickell et al., 2013; Pickell et al., 2015; Schneider et al., 2006). Landscape change affects all mid-size to large western boreal mammals living there (Fisher and Burton, 2018; Wittische et al., 2021), with effects most prominent in persistent woodland caribou (*Rangifer tarandus*) declines. Declines are caused by a complexity of interactions between predators, prey, and spatial features. Caribou are predated by wolves (*Canis lupus*) (Hebblewhite, 2017; Hervieux et al., 2013), which exploit a movement subsidy offered by extensive anthropogenic linear features (such as petroleum exploration "seismic" lines and roads) that enable faster travel and hence higher caribou encounter rates (Dickie et al., 2017; McKenzie et al., 2012). Simultaneously wolf populations are augmented *via* prey subsidies from high-density invading white-tailed deer (deer; *Odocoileus virginianus*) (Latham et al., 2013; Latham et al., 2011b), which themselves capitalize upon widespread early seral vegetation produced by anthropogenic landscape change (as well as climate change) (Fisher and Burton, 2021; Fisher et al., 2020; Laurent et al., 2021).

Past research in this complex region showed significant single-species responses to disturbance across the mammal community (Fisher and Burton, 2018), and subsequent multi-variate community analyses observed variance in relative abundance across space could be partially explained by relative abundance of heterospecifics (Wittische et al., 2021). We further explore the relationships between species' distribution, anthropogenic landscape features, and syntopic heterospecifics. We measured species' spatial distribution as 'occurrence frequency': the number of weeks (out of 3 years) a species is detected at a camera site. If a site is used more frequently, it is assumed to be of greater value (Manly et al., 2007). We hypothesized that, in addition to variance explained by anthropogenic landscape features, the occurrence frequency of: (1) caribou – as a species experiencing high predation pressure – would be best explained by predators and apparent competitors, with a negative relationship indicating spatial segregation; (2) moose (*Alces alces*) and deer, reliant on abundant forage, would be better explained by landscape features than by predators or apparent competitors; (3) wolves would be best explained by ungulate prey; (4) subdominant predators coyote (*Canis latrans*), lynx (*Lynx canadensis*), and fisher (*Pekania pennanti*) would be best (negatively) explained by the dominant competitor wolf, indicating spatiotemporal segregation; and (5) the large omnivore black bear (*Ursus americanus*) would be unaffected by syntopics due its wide niche breadth. We predicted these relationships to be synergistic (Darling and Côté, 2008), manifesting as interactions with anthropogenic landscape features: we predicted predators to respond more positively to linear-feature travel subsidies with increasing syntopic prey, and prey species to show a weaker positive (or even negative) response to forage-subsiding features (cutblocks, well sites) with increasing syntopic predators, as prey are expected to avoid these open features when predators are present.

## 2. Methods

2.1. Sampling frame and study area

Our sampling frame is the vast area of the Nearctic boreal forest termed the western Canada sedimentary basin (Porter et al., 1982). This landscape of aspen (*Populus tremuloides*), white spruce (*Picea glauca*), black spruce (*P. mariana*), and jack pine (*Pinus banksiana*) forests is interposed with *Rhododendron groenlandicum*-dominated muskeg in hydric areas. This boreal landscape maintains a diverse large mammal community including wolves, black bears, coyotes, lynx, fishers, white-tailed deer, moose, and caribou. Within this frame we surveyed mammal distribution in the Canadian oil sands of northeast Alberta, Canada (Fig. 1), an area of intensive and extensive anthropogenic landscape change. Extensive petroleum exploration and extraction features, roads (car accessible), trails (off-road vehicle accessible), timber harvesting, and other anthropogenic features occur throughout.

2.2. Sampling design

We deployed 61 camera-trap sites (Reconyx PC900 Hyperfire™ infrared remote digital; Holmen, WI, USA) in a constrained stratified random design (Fisher and Burton, 2018). The area was reclassified into four strata (aspen, conifer, high and low moisture reflecting major vegetational communities) and 1-km² sampling cells were randomly selected in equal proportions for each stratum. In each cell, one camera was placed on an active wildlife trail a minimum distance of 100-m from a road or trail. Though cameras were placed near roads and trails, these features are so ubiquitous that their proportion at small scales (within 250-m radius of a site) was not different from their proportion at larger spatial scales (within 5000-m radius of a site; Supplementary Information).

Following Burton et al. (2015), we define 'site' as the area in a radius of multiple spatial scales (circles of concentric radii; *sensu* Fisher et al. (2011)) centered on the camera detection zone. The 'study area' was the *ca.* 3500 km² minimum convex polygon surrounding camera sites. Cameras were placed *ca.* 1 m from the ground facing the wildlife trail and set to high sensitivity with 3-s delay. We sampled continuously between November 2011–November 2014.

Fig. 1. An array of 60 camera traps (blue dots) were deployed in the boreal forest of northeastern Alberta, Canada, 2011–2014 spanning natural heterogeneity and a gradient of areal anthropogenic features (such as forest harvest cutblocks; green polygons) and linear features (such as petroleum extraction "seismic" lines; grey lines).
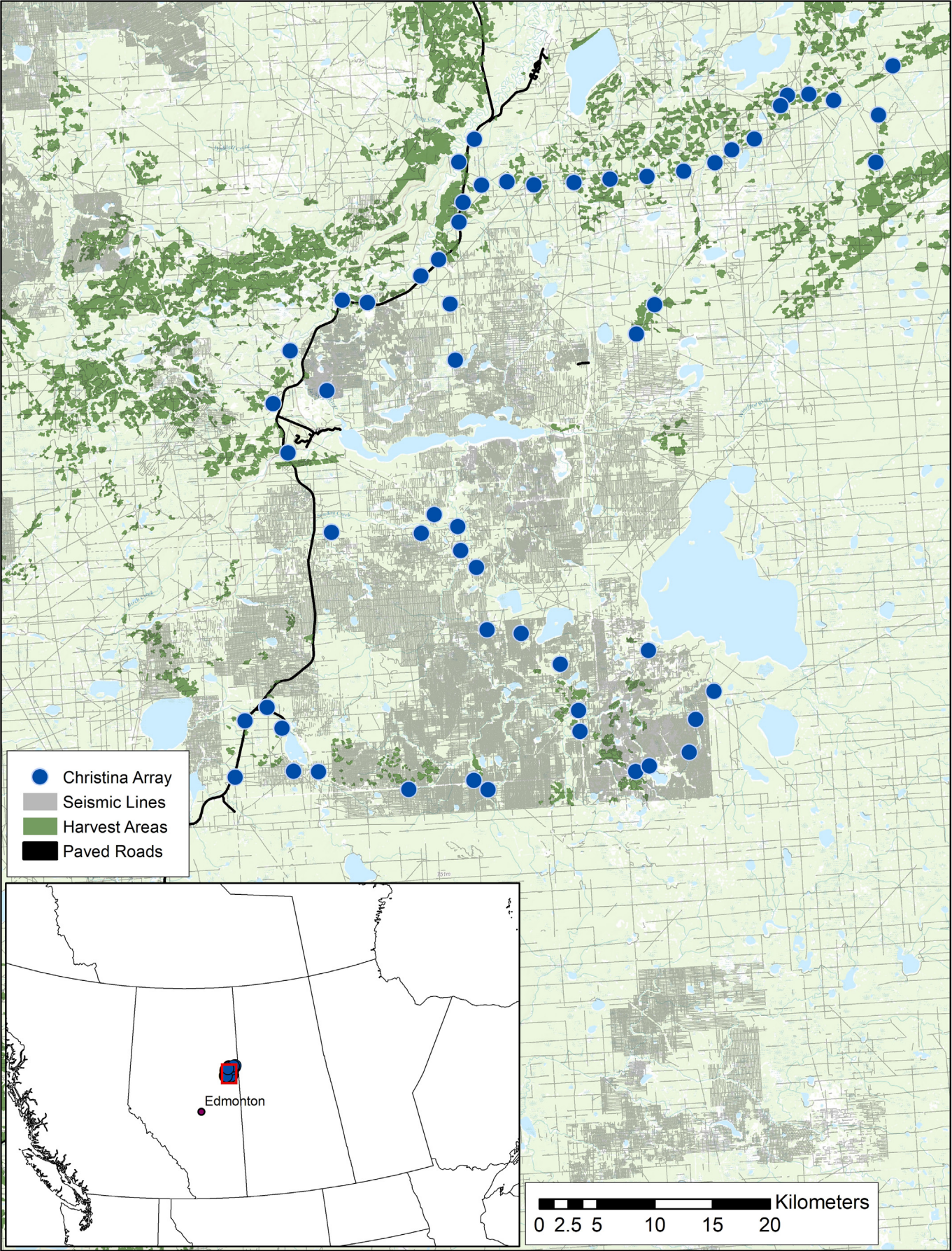
The 62,327 camera-trap days over 3 years produced 141,140 images of vertebrates, from which we calculated occurrence frequency: the number of monthly surveys (of 36) of each large (> 3 kg) mammal species present (Table 1). This discretization accounts for variable effort (due to occasional camera failures), and removes outliers in detection rates caused by repeat detections of lingering individuals or groups. Each month can be conceptualized as an independent Bernoulli trial in which the species was detected

Table 1

Competing hypotheses about the relative roles of landscape features and heterospecifics in explaining boreal mammal occurrence frequency. The core model for each species is the most parsimonious, best-supported model containing natural and anthropogenic landscape features (Table S1). "Heterospecific" models add occurrence frequency of a predator, prey, or competitor species to the core model. "Interaction" models add an interaction term to the heterospecific model: the anthropogenic feature with the greatest absolute effect size (positive or negative) from the core model. "Lines" = petroleum exploration seismic lines; "blocks" = industrial polygonal features including forest cutblocks and petroleum well sites.

Group	Species	Hypothesis	Heterospecific model	Interaction model
Carnivore	Wolf	Core model	None	None
		Prey 1	Caribou	Caribou*blocks
		Prey 2	Deer	Deer*blocks
		Prey 3	Moose	Moose*blocks
		Competitor 1	Coyote	Coyote*blocks
		Competitor 2	Lynx	Lynx*blocks
	Lynx	Core model	None	None
		Competitor 1	Wolf	Wolf*3D lines
		Competitor 2	Coyote	Coyote*3D lines
		Competitor 3	Fisher	Fisher*3D lines
		Prey 1	Deer	Deer*3D lines
		Prey 2	Moose	Moose*3D lines
	Coyote	Core model	None	None
		Dominant competitor	Wolf	Wolf*roads
		Prey 1	Deer	Deer*roads
		Prey 2	Moose	Moose*roads
		Competitor 1	Lynx	Lynx*roads
		Competitor 2	Fisher	Fisher*roads
Ungulate	Caribou	Core model	None	None
		Dominant predator	Wolf	Wolf*3D lines
		Alternate predator	Bear	Bear*3D lines
		Subdominant predator	Coyote	Coyote*3D lines
		Apparent competitor 1	Deer	Deer*3D lines
		Apparent competitor 2	Moose	Moose*3D lines
	Deer	Core model	None	None
		Dominant predator	Wolf	Wolf*cutblocks
		Alternate predator	Bear	Bear*cutblocks
		Subdominant predator	Coyote	Coyote*cutblocks
		Apparent competitor 1	Moose	Moose*cutblocks
		Apparent competitor 2	Caribou	Caribou*cutblocks
	Moose	Core model	None	None
		Dominant predator	Wolf	Wolf*wellsites
		Alternate predator	Bear	Bear*wellsites
		Subdominant predator	Coyote	Coyote*wellsites
		Apparent competitor 1	Deer	Deer*wellsites
		Apparent competitor 2	Caribou	Caribou*wellsites
Omnivore	Black Bear	Core model	None	None
		Competitor	Wolf	Wolf*3D lines
		Prey 1	Deer	Deer*3D lines
		Prey 2	Moose	Moose*3D lines
Scavenger	Fisher	Core model	None	None
		Dominant predator	Wolf	Wolf*3D lines
		Competitor 1	Coyote	Coyote*3D lines
		Competitor 2	Lynx	Lynx*3D lines
		Prey 1	Deer	Deer*3D lines
		Prey 2	Moose	Moose*3D lines

(1) or not (0) (Faraway, 2016), with each camera site as the unit of replication. We did not use occupancy models (MacKenzie et al., 2017) which assume the 0's in an (*e.g.*) 10101 detection history are error: because the models assume sites are closed to changes in occupancy during the sampling period, any positive detection (1) renders all 0's error. We have previously shown how 0's are in fact a signal of frequency of space-use due to animal movement (Stewart et al., 2018) and hence the signal we wish to model, not error to partition as probability of detection (*p*) as in occupancy models (Neilson et al., 2018).

2.3. Core model with natural and anthropogenic features

We built "core" models of landscape features expected to influence distribution but not related to hypotheses, based on known relationships (Fisher and Burton, 2018). We buffered camera locations with circles of 250-m to 5000-m radius in 250-m increments, *sensu* Fisher et al. (2011), within which we quantified the proportion (percent area) of landscape features: natural landcover (Alberta Vegetation Inventory, Government of Alberta), anthropogenic polygonal features (ABMI Human Footprint Ver.1.1, Alberta Biodiversity Monitoring Institute, 2010), and linear features (ABMI Caribou monitoring Unit, Alberta Biodiversity Monitoring Institute, 2012). Core variables included dominant forest type (deciduous, conifer, shrubland, *etc.*) by topography (upland or lowland), oil and gas exploration and extraction features (seismic lines, well sites), forest cutblocks, and roads (Supplementary Information, Table S1). We omitted correlated variables (Pearson's *r* > 0.7) (Zuur et al., 2010) by removing the rarer variable (usually pine forest) and scaled variables (mean = 0, s.d. = 1) to compare effect sizes.

We modelled species occurrence frequency against all landscape variables using generalized linear models (binomial errors, logit link) in *R* ver. 3.2.2 (R Foundation for Statistical Computing 2014) at the 20 spatial scales, and reduced the global model with the step-AIC function in R package *MASS* (Ripley et al., 2013). Akaike Information Criterion (AIC) score was calculated from the model's log likelihood, penalized by the number parameters. The lowest AIC score indicates the most-supported model, and hence the spatial scale at which natural and anthropogenic features best explain each species' occurrence frequency (Supplementary Information, Figs. S3 and S4).

From these best-supported core landscape models, we created sets of candidate models (Burnham and Anderson, 2002) by adding variables representing the occurrence frequency of syntopic heterospecifics, also measured as the proportion of months (of 36) the species was present at the camera site. We considered a species as syntopic if it occurred at the same camera site within the 36-month sampling duration, though in fact species typically co-occurred at least monthly, often weekly, sometimes daily. Each model we created represents a hypothesis about the influence of predators, prey, competitors, and apparent competitors (Table 1). Dominant predators (wolves) are primary predators of the prey species (deer, moose, caribou); alternate predators (black bears) also provide some predation risk. Subdominant predators (coyotes, lynx, fisher) provide a predation risk to prey, but are typically suppressed by the dominant predator (wolf). Apparent competitors do not compete directly for resources but share a predator with another prey species, such that increases in the apparent competitor increase the predator, decreasing the focal prey (Holt, 1977; Holt and Kotler, 1987). Here deer and moose are apparent competitors of caribou (DeCesare et al., 2010). The scavenger (fisher) is too small to predate the big prey though scavenges often; as do all the carnivore species (Peers et al., 2021).

To weigh evidence for synergistic effects between anthropogenic features and syntopic species, we created competing models with interaction terms among variables. For each species we noted the anthropogenic feature with the greatest absolute effect size in the core model – which we had predicted would reflect either resource subsidies or the greatest risk – and added an interaction term between each heterospecific and that anthropogenic feature variable. We weighed evidence in support of candidate models based on ΔAIC and normalized AIC weights. Following the

philosophy of Burnham and Anderson (2002) the best-supported models are those with ΔAIC = 0; however models with small nonzero ΔAICs are not necessarily rejected but offer alternatives with some degree of support, quantified as AIC weights (AIC$_w$). AIC$_w$ are ΔAICS normalized as $L(g_i|x)$, considered as the weight of evidence in favor of model i being the actual best model describing the data (given that one of the set must be the best model from that set) (Burnham and Anderson, 2002). Models that share AIC$_w$ are thus considered to share some likelihood of being the most-supported model.

We validated the models with highest AIC$_w$ using k-fold cross validation (Roberts et al., 2017) in the *cv.glm* function in the R package *boot* (Canty, 2002), including the adjusted delta, which represents the relative prediction error between competing models while accounting for bias introduced by the k-partitioning (Davison and Hinkley, 1997).

3. Results

In 36 months we detected wolves (2508 images), black bears (2657), moose (500), white-tailed deer (112648), coyote (2290), lynx (1940), red fox (197), fisher (326), and caribou (273). Detections were recorded from every site, though variably for each species.

3.1. Model selection

The core model and relevant spatial scale of selection varied for each species (Supplementary Information Figs. S3 and S4). Anthropogenic linear features, polygonal features, or both, explained occurrence frequency of every species, in addition to natural landcover covariates, and are explained in depth by Fisher and Burton (2018).

Heterospecific co-occurrences were important for every boreal mammal species except caribou and fisher: models including syntopic species and (or) their interactions shared a majority of AIC weight for wolves, lynx, coyotes, deer, moose, and black bears (Table 2). The additive effect of heterospecifics was sometimes indiscernible from the interaction effect, as AIC$_w$ was shared across additive and interaction models in a number of cases (Table 2). Black bears and coyotes had top models with relatively high AIC$_w$ (0.36 and 0.41 respectively); in contrast caribou and fisher AIC$_w$ were widely distributed across a number of different models

Table 2

Model selection table, ranking support for competing models corresponding to hypotheses outlined in Table 1. Boreal mammal occurrence frequency was modelled in conjunction with landscape features and the occurrence of heterospecifics. The core model is the most parsimonious, best-supported model containing natural and anthropogenic landscape features. Heterospecific models (dominant predator, *etc.*) included the core landscape model plus occurrence frequency of the heterospecific. Interaction terms were selected as the anthropogenic feature with the greatest absolute effect size in the core model. Int. = interaction with landscape feature (Table 1).

Group	Species	model name	AIC	ΔAIC	AIC$_w$	K-fold Δerror
Carnivore	Wolf	Prey deer int.	281.30	0.00	0.39	0.01
		Prey deer	282.03	0.73	0.27	0.01
		Prey moose	284.27	2.97	0.09	0.01
		Core landscape	285.03	3.73	0.06	0.01
		Competitor lynx	285.09	3.79	0.06	0.01
		Prey moose int.	286.26	4.96	0.03	0.01
		Prey caribou	286.94	5.65	0.02	0.01
		Prey caribou int.	287.57	6.27	0.02	0.01
		Competitor coyote	286.99	5.69	0.02	0.01
		Competitor lynx int.	287.01	5.71	0.02	0.01
		Competitor coyote int.	288.22	6.92	0.01	0.01
	Lynx	Prey moose	266.51	0.00	0.73	0.00
		Prey moose int.	268.45	1.94	0.27	0.00
		Core landscape	353.98	87.48	0.00	0.02
		Dominant competitor wolf	355.88	89.37	0.00	0.02
		Dominant competitor wolf int.	348.25	81.75	0.00	0.02
		Prey deer	354.83	88.33	0.00	0.02
		Prey deer int.	356.61	90.11	0.00	0.02
		Competitor coyote	341.69	75.19	0.00	0.02
		Competitor coyote int.	335.21	68.71	0.00	0.01
		Competitor fisher	354.06	87.56	0.00	0.02
		Competitor fisher int.	352.78	86.27	0.00	0.02
	Coyote	Prey moose int.	356.94	0.00	0.41	0.02
		Competitor lynx int.	357.47	0.53	0.32	0.02
		Competitor lynx	357.96	1.02	0.25	0.02
		Prey moose	363.76	6.82	0.01	0.02
		Core landscape	383.43	26.50	0.00	0.02
		Dominant competitor wolf	381.63	24.69	0.00	0.02
		Dominant competitor int.	366.27	9.33	0.00	0.02
		Prey deer	383.63	26.69	0.00	0.02
		Prey deer int.	377.81	20.87	0.00	0.02
		Competitor fisher	381.66	24.72	0.00	0.02
		Competitor fisher int.	381.67	24.73	0.00	0.02
Prey	Caribou	Core landscape	49.60	0.00	0.23	0.02
		Alternate predator bear	50.41	0.81	0.15	0.03
		Subdominant predator coyote	51.28	1.68	0.10	0.03
		Dominant predator wolf	51.45	1.85	0.09	0.05
		Apparent comp deer	51.54	1.94	0.09	0.02
		Alternate predator bear int.	51.58	1.99	0.08	0.05
		Apparent comp moose	51.59	2.00	0.08	0.05
		Apparent comp deer int.	52.25	2.65	0.06	0.06
		Dominant predator wolf int.	52.83	3.23	0.05	0.02
		Subdominant predator coyote int.	53.11	3.52	0.04	0.07
		Apparent comp moose int.	53.15	3.55	0.04	0.06

(continued on next page)

Table 2 (*continued*)

Group	Species	model name	AIC	ΔAIC	AIC$_w$	K-fold Δerror
	Deer	Apparent comp caribou	351.76	0.00	0.46	0.02
		Apparent comp caribou int.	352.97	1.21	0.25	0.03
		Dominant predator wolf int.	353.22	1.46	0.22	0.02
		Dominant predator wolf	356.58	4.82	0.04	0.02
		Core landscape	360.62	8.86	0.01	0.02
		Subdominant predator coyote int.	360.65	8.89	0.01	0.02
		Alternate predator bear	362.62	10.86	0.00	0.02
		Alternate predator bear int.	362.52	10.76	0.00	0.02
		Subdominant predator coyote	362.14	10.38	0.00	0.02
		Apparent comp moose	361.87	10.11	0.00	0.02
		Apparent comp moose int.	363.23	11.47	0.00	0.02
	Moose	Subdominant predator coyote	335.44	0.00	0.30	0.02
		Subdominant predator coyote int.	337.38	1.93	0.12	0.02
		Dominant predator wolf	337.45	2.00	0.11	0.01
		Dominant predator wolf int.	337.89	2.44	0.09	0.02
		Core landscape	338.21	2.77	0.08	0.02
		Apparent comp caribou	338.04	2.59	0.08	0.02
		Apparent comp deer int.	338.29	2.85	0.07	0.01
		Alternate predator bear int.	339.23	3.79	0.05	0.01
		Alternate predator bear	339.84	4.40	0.03	0.02
		Apparent comp deer	339.88	4.44	0.03	0.02
		Apparent comp caribou int.	339.89	4.45	0.03	0.02
Omnivore	Bear	Prey moose int.	289.29	0.00	0.36	0.02
		Core	290.28	0.98	0.22	0.02
		Prey deer	291.43	2.14	0.12	0.02
		Prey moose	291.48	2.19	0.12	0.02
		Dominant competitor wolf	292.27	2.98	0.08	0.02
		Prey deer int.	293.23	3.94	0.05	0.01
		Dominant competitor wolf int.	293.96	4.67	0.04	0.02
Scavenger	Fisher	Prey moose	218.32	0.00	0.19	0.00
		Prey deer	218.83	0.51	0.15	0.00
		Competitor coyote	219.00	0.68	0.14	0.00
		Competitor lynx	219.67	1.35	0.10	0.00
		Core	219.86	1.54	0.09	0.00
		Prey moose int.	220.07	1.75	0.08	0.00
		Prey deer int.	220.30	1.98	0.07	0.00
		Dominant competitor wolf	220.91	2.58	0.05	0.00
		Competitor coyote int.	220.83	2.51	0.05	0.00
		Dominant competitor wolf int.	221.30	2.98	0.04	0.00
		Competitor lynx int.	221.67	3.35	0.04	0.00

(Table 2), meaning no model(s) were clearly better supported than others. For brevity we plotted β coefficients from models with the highest AIC$_w$ (though other models may share support).

3.2. Carnivores

Wolf occurrence frequency was best explained by white-tailed deer occurrence interacting with anthropogenic block features (Table 2). Wolves were more likely to occur at sites with block (polygonal) petroleum features: industrial camps, extraction facilities, and associated features (Fig. 2a). Wolves' positive relationship with block features increased with increasing white-tailed deer occurrence frequency, and *vice versa*: the relationship with white-tailed deer increased with increasing proportion of block features on the landscape ($\beta_{Block*deer}$ = 0.20, Standard Error (SE) = 0.12; Fig. 3).

Lynx occurrence frequency was best explained by moose occurrence, after accounting for landscape features (Fig. 2), and the effect size was large relative to the other variables included in the top model (β_{moose} = 0.70, SE = 0.077; Fig. 3).

Coyotes were more likely occur at sites with higher moose occurrence (β_{moose} = 0.32, SE = 0.067; Fig. 2a) after accounting for landscape features. Coyotes' relationship with road density increased more steeply as moose occurrence frequency increased, and *vice versa* ($\beta_{Road*moose}$ = 0.22, SE = 0.075; Fig. 3).

3.3. Ungulate prey

Caribou occurrence frequency was best explained by landscape features (Fig. 2b); the inclusion of heterospecifics did not increase model support by

explaining added variability (Table 2). In contrast to predictions, caribou occurrence frequency was not explained by wolf occurrence frequency.

White-tailed deer occurrence frequency was best explained by its apparent competitor, woodland caribou ($\beta_{caribou}$ = −0.191, SE = 0.059; Fig. 3), in addition to landscape features (Fig. 2b). Deer and woodland caribou segregated on this landscape, even after accounting for differences in habitat selection.

Moose occurrence frequency was explained by subdominant predators (coyotes) as well as landscape features (Fig. 2b). Moose and coyote positively co-occurred (β_{coyote} = 0.13, SE = 0.059; Fig. 3), as also reflected in the coyote models. In contrast to predictions, wolves and black bears as the dominant predators did not best (negatively) explain the frequency of occurrence of moose as a prey species.

3.4. Omnivores and scavengers

Occurrence frequency of black bear – an omnivorous predator – was related to multiple landscape features, but only weakly (Table 2; Fig. 2c). Bears were negatively related to 3D seismic lines, but this effect size decreases with increasing moose occurrence; in fact the direction of the relationship with 3D seismic lines changes between low moose occurrence (strongly negative relationship) and high moose occurrence (strongly positive) (Fig. 3). This prey-interaction model carries 36% of the AIC$_w$, compared to 22% of the landscape-only core model (Table 2). Evidence that fisher – which scavenge from large-mammal kills by other predators – is affected by syntopics is ambiguous, as model AIC$_w$ is shared among models with moose, deer, coyote, lynx, as well as the core (landscape-only) model (Table 2). Because of this lack of clear signal we illustrate only fishers' relationship to landscape features (Fig. 2c).
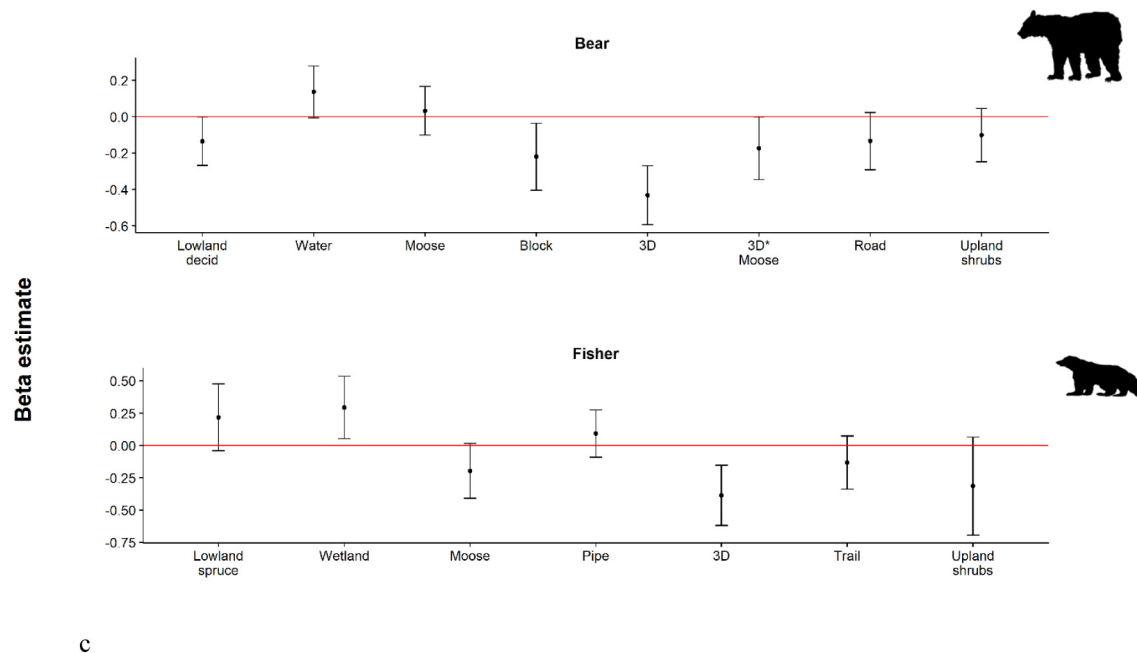
a

b
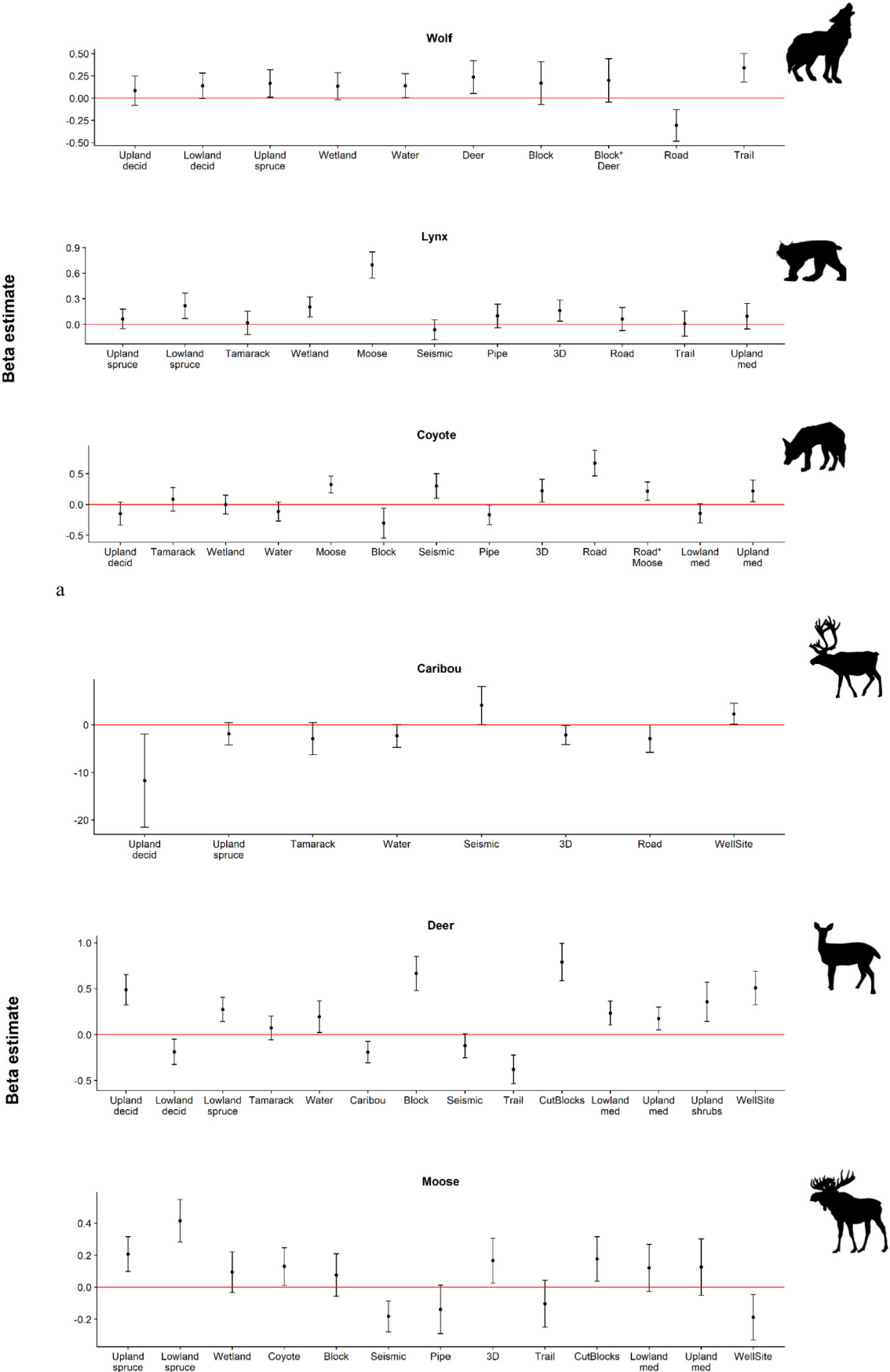
Fig. 2. a. β coefficients from the best-supported models of carnivore occurrence frequency in relation to natural landcover, anthropogenic landscape features, heterospecific occurrence frequency, and interaction terms, which are denoted as: feature*heterospecific. A positive interaction term means the slope of mammal-landscape regression line increases with increasing heterospecific occurrence. Bars represent confidence intervals (1.96 * Standard Error). b. β coefficients from the best-supported models of prey occurrence frequency in relation to natural landcover, anthropogenic landscape features, heterospecific occurrence frequency, and interaction terms, which are denoted as: feature*heterospecific. A positive interaction term means the slope of mammal-landscape regression line increases with increasing heterospecific occurrence. Bars represent confidence intervals (1.96 * Standard Error). c. β coefficients from the best-supported models of omnivore and scavenger occurrence frequency in relation to natural landcover, anthropogenic landscape features, heterospecific occurrence frequency, and interaction terms, which are denoted as: feature*heterospecific. A positive interaction term means the slope of mammal-landscape regression line increases with increasing heterospecific occurrence. Bars represent confidence intervals (1.96 * Standard Error).

4. Discussion

Most large boreal mammals' response to pervasive landscape change is significantly affected by co-occurring prey, competitors, or apparent competitors; these syntopic heterospecifics act synergistically with landscape features for some species, and not for others. The influence of syntopic species on an animal's spatial distribution supports realized niche theory, wherein interacting heterospecifics truncate a species' fundamental niche (Colwell and Rangel, 2009; Hutchinson, 1957). We contend that heterospecific syntopy likely influences species-habitat relationships across ecological systems: a recently emerging concept (Godsoe and Harmon, 2012) but laden with analytical complexities. Of course syntopy does not strictly result in ecological interactions; false assumptions can lead to specious conclusions, but a reasonable framework for hypothesizing interactions can overcome these challenges (Blanchet et al., 2020). We based our hypotheses (Table 1) on known relationships among heterospecifics (Benson and Patterson, 2013; DeCesare et al., 2010; Fisher et al., 2020; Latham et al., 2011a; Latham et al., 2011b; Squires and Ruggiero, 2007; Wasser et al., 2011), and encourage this same framework in studies of syntopy in other systems and species assemblages.

A multi-species approach yields important insights. We predicted that dominant predators would exert the largest influence on prey distribution, and *vice versa*. Only half of this prediction was supported. Predators were better explained by prey heterospecifics, after accounting for landscape features; however, the large ungulates were explained by apparent competitors (deer, by caribou, with a weaker effect of wolves) and subdominant predators (moose, by coyotes). Relationships were not reciprocal, except for wolves and coyotes. For example, although wolf distribution was best explained by deer, deer distribution was more weakly explained by wolves, but better explained by caribou. Caribou-deer spatial segregation is very likely the outcome of both differential habitat selection (accounted for in the core models) as well as separation as an anti-predator behaviour,

observed elsewhere for caribou and moose (James et al., 2004). Spatial segregation has been observed for mammals in multiple terrestrial (Fisher et al., 2013; Mori and Menchetti, 2019; Sozio and Mortelliti, 2016; Wereszczuk and Zalewski, 2015) and marine (Fisher et al., 2014) systems. Notably there was no clear effect of syntopic heterospecifics for caribou; though we expected predators to drive caribou distribution this was not supported, either due to very small sample sizes or because landscape features are indeed more important (Boutin et al., 2012).

Most notably, the movement subsidies imparted by anthropogenic linear features (Dickie et al., 2017; Whittington et al., 2011) is more heavily selected by predators where prey abundance is high. This effect size is particularly great for anthrophilic coyotes, but also important for dominant wolves. This suggests that anthropogenic features are facilitating predation on ungulates. Linear features do facilitate wolf travel (Dickie et al., 2017) but this is the first spatial signal of interactions between anthropogenic features, predators, and prey, and provides insights into how landscape change triggers spatial declines (and by inference, population declines) that may presage future biodiversity losses.

In contrast to our predictions, competitors did not appear to influence boreal mammals' distributions after accounting for differential habitat selection. This is surprising, as (for a northern ecosystem) there are high relative abundances of each of the species studied (Burgar et al., 2019), and we might expect rigorous competition. Competitor syntopy is important for other mammal species and systems (Davis et al., 2018; Di Bitetti et al., 2010; Farris et al., 2016; Fisher et al., 2013; Rich et al., 2017). However, a similar lack of signal of competition has been found in northern mammal studies (Dyck et al., 2022; Schmidt et al., 2009; Wikenros et al., 2010) as well as many plant (Brazeau and Schamp, 2019) and insect (Giller and Doube, 1994) communities. We infer from our results that competition plays less of a role in spatially structuring boreal mammal communities than do anthropogenic landscape features and predator-prey relationships.
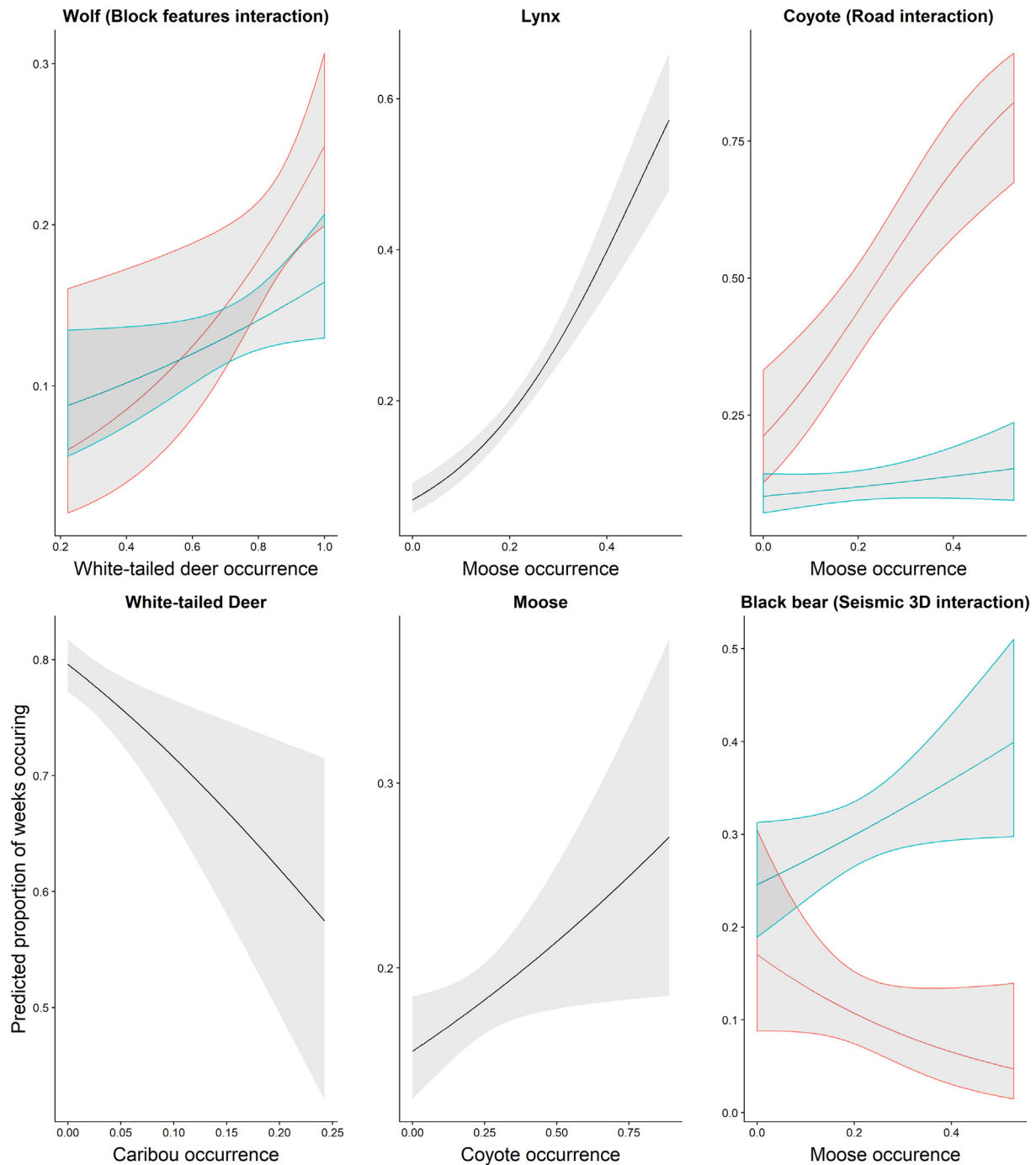
Fig. 3. The relationship between the predicted proportion of weeks each species occurred and landscape features, heterospecifics (in the form of frequency of occurrence), and their interaction, from best-supported models for each species. Where an interaction was present, we calculated based on the 5th (low – blue) and 95th (high – red) percentiles for the interacting variable.

The effect of syntopic species is less (or not) apparent for omnivores and mustelid predators. Although black bears predate caribou, deer, and moose, predation is opportunistic and this landscape offers diverse omnivorous diet choices. Black bears respond negatively to some anthropogenic features (Fisher and Burton, 2018) and we show that the presence of moose (prey) changes the direction of this relationship: at high moose occurrence frequency black bears increase with increased 3D seismic lines (Fig. 3). This signal was weak however, and we infer that bears' diverse diet (Pelchat and Ruff, 1986; Raine and Kansas, 1990) allowed them to exploit a wide array of food sources largely irrespective of heterospecifics.

Moreover fishers – which prey on small mammals (Weir et al., 2005; Zielinski and Duncan, 2004) but opportunistically scavenge (Powell and

Zielinski, 1994) – likewise showed no effect of large mammal co-occurrence. Further exploration may reveal a role for smaller mammal prey, though it is surprising that the several larger competitors in this system played no role in fishers' occurrence frequency across this landscape.

We had predicted that the relationships between heterospecifics would be mediated by anthropogenic landscape features; specifically, that prey would be influenced by predators more strongly with high densities of linear features as a travel subsidy (Dickie et al., 2017; McKenzie et al., 2012) and block features as a prey-forage subsidy (Fisher and Burton, 2018; Fisher et al., 2020). In fact the clearest signal of interactions with anthropogenic features are from coyotes, a highly anthrophilic species (Hody and Kays, 2018) exploiting features across multiple boreal systems (Heim et al.,

2019; Tattersall et al., 2020). Moose selected forestry cutblocks (as elsewhere; (Fisher and Wilkinson, 2005)) but increasingly avoided cutblocks as coyotes increased. Likewise coyotes more strongly selected roads as moose increased. Other heterospecific pairs showed some weak evidence of interaction with anthropogenic features worth further exploration.

4.1. Caveats

We did not compete all possible combinations of heterospecifics, landscape features, and interaction terms against one another. We assiduously sought to avoid such a "data dredge" and instead built hypothesis-based models (Burnham and Anderson, 2002). By the same token we did not compete landscape-only core models against heterospecific-only models as the comparison would have been highly unbalanced: the landscape models represent the best-supported models containing up to 18 variables from a set of 20 different spatial scales as in Fisher and Burton (2018). Competing these models against a heterospecific model with only 1–2 variables confounds evaluating the ecological process with the statistical process from which the models arose. We caution that, as with all model selection analyses, our conclusions are limited to the candidate set; a different set – such as using more interaction terms for more industrial variables – might yield different insights. Finally, our results stem from a large but single landscape, and we encourage further examination across multiple landscapes with different communities, natural heterogeneity, and degrees of landscape change to determine if conclusions hold more generally.

5. Conclusions

Boreal anthropogenic landscape change delivers more than predator travel and ungulate resource subsidies: industrial features can provide subsidies for interspecific predator-prey interactions, extending well beyond the current wolf-caribou paradigm. Wolves' syntopy with white-tailed deer synergistically increases with industrial block features; coyotes' syntopy with moose synergistically increases with roads. Anthropogenic resource extraction changes more than landscapes: it changes the spatial outcomes of interactions among wildlife species.

Boreal mammals' synergistic relationship to landscape change and syntopic species conforms to predictions from niche theory (Colwell and Rangel, 2009; Hutchinson, 1957): the realized niche-space molded by interspecific processes differs from the fundamental niche space where an organism could exist without heterospecifics. Conceptually the role of heterospecifics in species-distribution models has been lately recognized (Araujo and Guisan, 2006; Godsoe and Harmon, 2012); though recent works have cautioned about inferring interspecific processes from co-occurrence patterns, they have also provided guidance about how to strengthen these inferences (Blanchet et al., 2020; Peterson et al., 2020; Thurman et al., 2019). We contend that including interacting syntopic species in analyses of species' response to landscape change will yield critical insights currently missing – with the usual caveats about inferring causation from correlation. Here we show signals of apparent competitors and subdominant predators that have not been considered in previous research on the effects widespread landscape change on mammalian biota. Research on the effects of pervasive global landscape change on biota (Maxwell et al., 2016) requires a community ecology approach that integrates spatial landscape processes. Currently, ecology and conservation tend toward focal species (Lindenmayer et al., 2002; Simberloff, 1998) and a major shift to explicitly measure and model entire wildlife communities required.

Authors' contributions

JTF conceived the original research, designed the camera array, fundraised, and supervised data collection and analysis. AL conducted statistical analyses. Both authors conceived and wrote this paper, reviewed and edited the drafts, and gave final approval for publication.

Research ethics

Data collection was permitted by the Government of Alberta, Ministry of Environment and Parks, Fish & Wildlife Division, Collection License 49143.

Animal ethics

This research was reviewed and approved by InnoTech Alberta's Animal Care and Use Committee (ACUC), permit ACUC0524.frm/clj/IO.II.02.

Data accessibility

All data used are publicly available on Dryad: doi:https://doi.org/10.5061/dryad.xksn02vf2.

CRediT authorship contribution statement

Jason T. Fisher: Conceptualization, Methodology, Investigation, Writing – original draft, Writing – review & editing, Supervision, Supervision, Funding acquisition. **Andrew Ladle:** Software, Validation, Formal analysis, Resources, Data curation, Visualization, Writing – review & editing.

Declaration of competing interest

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

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.153432.

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