



Landscape change shifts competitive dynamics between declining at-risk wolverines and range-expanding coyotes, compelling a new conservation focus[☆]

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ABSTRACT

Conservation actions need to target ecological mechanisms of species declines to be effective, but these mechanisms are often opaque. Shifting balance of competition is one pathway to species declines. Competitive coexistence is maintained only where competitive pressures balance across space. As resources change and new resources are introduced or disappear across landscapes, so should competition outcomes. We tested how novel anthropogenic disturbances affect this competitive landscape in a region with a diverse large carnivore community. We modelled fine-resolution spatiotemporal co-occurrence of wolverine (*Gulo gulo*), an at-risk Nearctic facultative scavenger, and other competing carnivores. We posed hypotheses about the different interspecific interactions – competition, predation, and facilitation – that could affect wolverine distribution across a gradient of anthropogenic disturbance. We used an information-theoretic model-selection framework to weigh evidence for hypotheses about the outcomes of interspecific interactions, inferred from habitat selection in relation to co-occurrence or segregation with other carnivores. Wolverine occurrence in space and time was explained by anthropogenic disturbance features and coyote co-occurrence at sites, revealing that coyote occurrence is a synergistic factor with anthropogenic disturbance. Wolverine were generally segregated from coyotes and avoided linear features; however if wolverine and coyotes did co-occur, they were twice as likely to co-occur at sites with linear features. Thus linear features increased opportunity for coyotes—a generalist species thriving in human disturbed landscapes – to compete with wolverines. We suggest this threat of increased competition is a mechanism potentially contributing to broad-scale wolverine range recessions from increasingly disturbed areas. Landscape change manifests as more than just physical disturbances: it alters the ecological processes that structure communities. These processes contribute to declines of species that cannot adapt to the novel disturbance features. We emphasize competition as an overlooked outcome of landscape change that could inform better conservation decisions to stem species declines.

1. Introduction

Conservation actions need to target the mechanisms of species declines to effectively maintain biodiversity (Norris, 2004) but those mechanisms are often opaque and inferred from changes to population size or distribution. In North America, large carnivores have decreased across their range since European colonization (Laliberte and Ripple, 2004) and of particular conservation concern are wolverines (*Gulo gulo*):

the contiguous USA range is very restricted and wolverines have been extirpated from all of eastern Canada. Mechanisms of decline are debated. Population declines and historical range reductions have been linked to decreases in snow cover (Brodie and Post, 2010; Copeland et al., 2010), and with warming winters, climate change is expected to further reduce wolverine range (McKelvey et al., 2011). The relationship to snow was the basis of a recent petition to list under the United States' Endangered Species Act, overturned in part due to lack of confidence in

[☆] **Impact statement:** Landscape change indirectly affects competition to the detriment of species that cannot adapt to disturbances; a mechanism that can inform species declines.

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this mechanism. In Canada however, anthropogenic disturbance features are negatively related to wolverine distributions, playing a role apparently greater than snow (Fisher et al., 2013; Stewart et al., 2016; Scrafford et al., 2017; Heim et al., 2017). However, wolverines do not behaviourally avoid anthropogenic landscape features, implicating some other proximal mechanism behind wolverines' negative association with disturbance.

Recent emerging evidence suggests interspecific interactions play an important role in structuring wolverine behaviour (Fisher and Bradbury, 2014; Stewart et al., 2016), and distribution (Heim et al., 2017, 2019) in North America, as well as in Scandinavia (Andr  n et al., 2011; Mattisson et al., 2011a, 2011b). In theory, differences in habitat selection between competing species allow for competitive coexistence on patchy landscapes (Chesson, 2000), causing species to spatially and temporally segregate, maintaining broad-scale sympatry (Amarasekare, 2003; Armstrong and McGehee, 1976; Chesson, 1985). Interspecific interactions can drive broad-scale spatial and temporal segregation, and conversely, co-occurrence (Fisher et al., 2012; Linnell and Strand, 2000; Sunarto et al., 2015), depending on the trade-off between the costs of co-occurrence at high-quality sites or segregation into poorer-quality sites. As global landscapes change (Maxwell et al., 2016) the spatial pattern of resources affecting species distributions is altered (Foley et al., 2005; Pickell et al., 2016). Changes in resources that govern interspecific interactions will variably affect strength and direction of those interactions (Berger, 2007; Bowman et al., 2010; Wang et al., 2015). If interspecific interactions are the mechanism behind declines, they need to be the target for conservation actions.

In the Nearctic boreal forest, anthropogenic disturbance features can change resource availability and species' acquisition of resources by introducing forage subsidies (Fisher and Wilkinson, 2005), or creating travel corridors through otherwise complex habitat (Dickie et al., 2017). Some carnivores—such as wolverines—are “losers” and suffer range contractions from landscape change (Fisher et al., 2013; Heim et al., 2017), whereas other species—such as coyotes (*Canis latrans*)—are “winners” that can exploit novel resources (Fisher and Burton, 2018; Hody and Kays, 2018). The effects of landscape change on biodiversity are often understood through trends in habitat loss (Butchart et al., 2010), or changes in trophic relationships, such as apex predator declines (Estes et al., 2011). However, increased co-occurrence within a competing carnivore community may also adversely influence biodiversity.

The effects of anthropogenic features on interspecific interactions are challenging to quantify across large landscapes under natural conditions. First, mammalian species co-occurrences at large spatial scales are hard to observe; this has only recently been made possible with remote camera traps (Burton et al., 2015). Second, species co-occurrences can be used to infer interactions, but only if conducted under a weight-of-evidence paradigm based on clearly articulated hypotheses, rather than a data dredge (Blanchet et al., 2020; Peterson et al., 2020; Thurman et al., 2019). Third, contemporary patterns of species spatial segregation could be driven in large part by historical competition—sometimes called the “ghosts of competition past” (Rosenzweig, 1991)—where the two species have differential realized habitat use mediated by past competition, and are no longer syntopic. We contend that examining temporal co-occurrence patterns over short time frames in areas of syntopy allows one to parse apart the contribution of heterospecifics to variation in probability of occurrence: *sensu* Tattersall et al. (2020a). Here, we examine trends in weekly spatiotemporal co-occurrence—or conversely, segregation—in the carnivore community in the Rocky Mountains of western Canada. One week is the time needed for an adult wolverine to patrol its home range (Scrafford and Boyce, 2018) and is a reasonable proxy for syntopy given carnivore movement rates.

We modelled wolverine occurrence using a spatially- and temporally-explicit approach incorporating carnivore heterospecifics, building on previous analyses of wolverine habitat selection (Heim et al., 2019). We weighed evidence for three different processes affecting

wolverine spatiotemporal distribution—competition, predation, and facilitation—and how disturbance features affect these interspecific interactions. We hypothesize that wolverine habitat selection is affected by interactions with interspecific carnivores, with the interactions varying with type and density of anthropogenic features. Our core or ‘null’ model—no effect of heterospecifics—described spring snow cover which varies with topography and elevation. We hypothesized spatiotemporal segregation from coyote (*Canis latrans*) and red fox (*Vulpes vulpes*) as a result of competition; previously spatial but not temporal segregation has been observed (Heim et al., 2017; Heim et al., 2019). We hypothesized spatiotemporal segregation from grey wolves (*Canis lupus*) and cougar (*Puma concolor*) (Krebs et al., 2004), to avoid predation. We hypothesized spatiotemporal co-occurrence with lynx (*Lynx canadensis*) as a function of facilitation; Palearctic wolverines benefit by scavenging *Lynx lynx* kills (Andr  n et al., 2011; Mattisson et al., 2011a; Mattisson et al., 2011b). Finally we hypothesized that anthropogenic landscape features could mediate competition, predation, or facilitation.

We weighed evidence for competing models whereby variation in wolverine occurrence is explained by: 1) anthropogenic disturbance features, 2) segregation from grey wolf and/or cougar, signalling role of predation risk, 3) co-occurrence of coyote and/or red fox, signalling competition risk, and 4) co-occurrence with lynx, signalling facilitation. Further, we hypothesized anthropogenic features affected all three of the interspecific interactions. By homing in the mechanisms causing declines, we can inform conservation actions that mitigate the anthropogenic impacts affecting these mechanisms, and stand a better chance of conserving this increasingly rare species.

2. Methods

2.1. Study areas

Similar to previous studies of wolverine and syntopic carnivore behaviour (Frey et al., 2020; Stewart et al., 2016) we capitalized on existing camera trap data from two identically designed studies of wolverine abundance and distribution in the Rocky Mountains of Alberta, Canada, in the Willmore Wilderness Park and Kananaskis Country (Fisher et al., 2013; Heim et al., 2017) (Fig. 1). Both landscapes supports a similarly diverse carnivore community (Fisher et al., 2011; Heim, 2015). The Willmore Wilderness Park (WW) is a conservation area with minimal anthropogenic disturbance located on the Front Range of the Rocky Mountains. Comparatively, the nearby Kananaskis Country (KC) in the East Slopes of the Rocky Mountains has much more varied legislative protection and land-use practices for resource extraction and recreation. Both are dominated by mature coniferous forests and small deciduous stands, and have similar snow regimes (Supplementary Information S1). However WW is protected from landscape development, with only limited access and restricted motorized vehicle use. KC is managed for tourism and recreation, industrial development, and transportation—resulting in 86-fold greater polygonal disturbance feature density, and 26-fold greater linear feature density (Supplementary Information S1).

2.2. Collection of carnivore occurrence data

Reconyx™ heat-in-motion digital cameras (models RM30, PM30, PC900; Reconyx, Holmen, WI) were used to sample species occurrence within an area defined by the camera's detection cone. Cameras on both landscapes were distributed in a systematic sampling design based on 144 km² square grid cells, approximating a female wolverine home range. This design aimed to capture the range of landscape heterogeneity experienced by an average wolverine; the probabilistic design provides rationale for extrapolating inference across the area—with the usual caveats about interpreting spatial scale (Wheatley and Johnson, 2009)—with inference derived from the point location. Within each cell we placed one camera at natural features (avalanche chutes, creek beds)

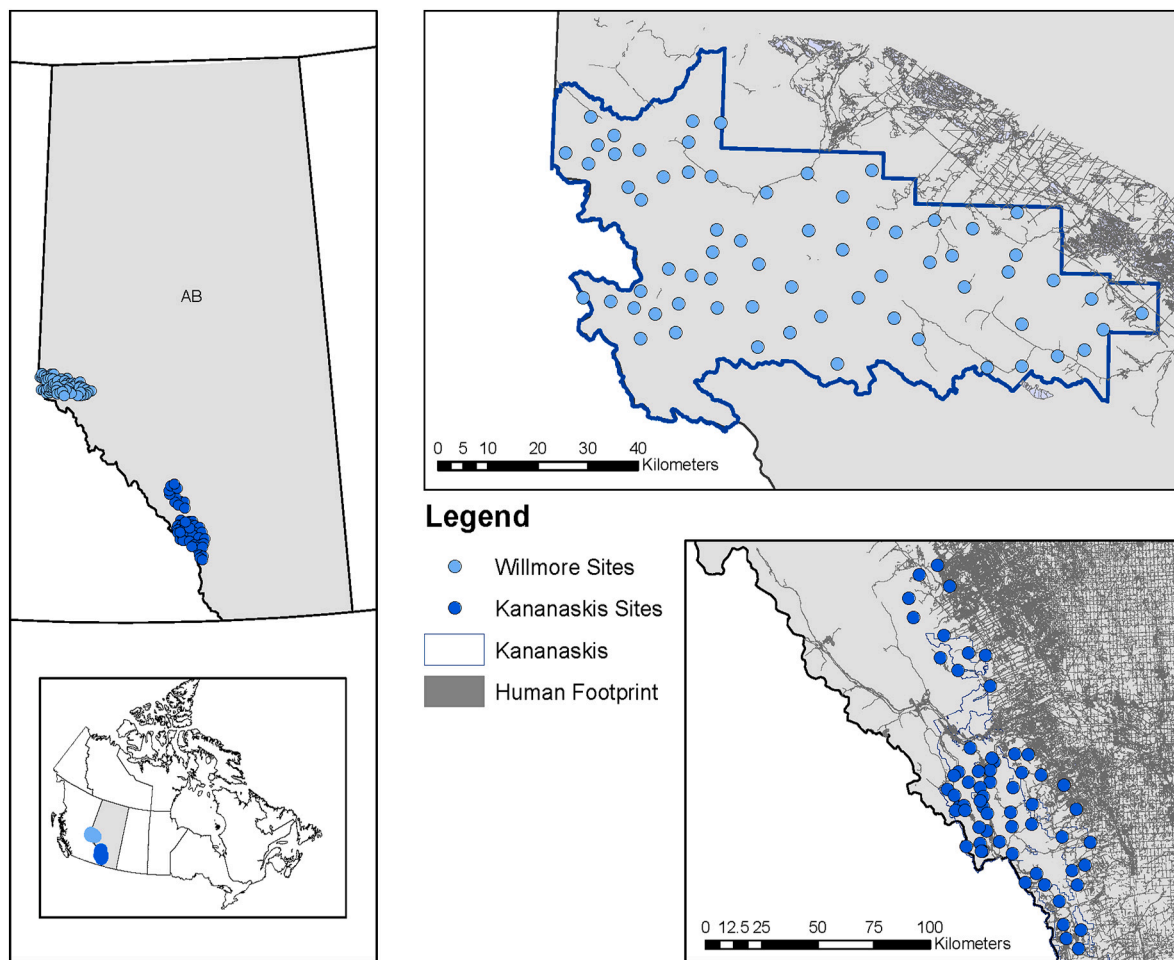


Fig. 1. Camera trap locations in the Willmore Wilderness Park (WW) (top panel) and Kananaskis Country (KC) in the East Slopes of the Rocky Mountains (bottom panel).

intended to maximize probability of species detection given presence, but constrained by helicopter access and avalanche risk; for more design details see [Fisher and Bradbury \(2014\)](#). Cameras were placed ca. 1.5 m up a tree and set to high sensitivity with no delay between subsequent detections.

Cameras were deployed for two winter seasons in the WW for 13 weeks from December 15 to March 15 (2006–07, 2007–08), and for 22 weeks in KC from December 1 to March 30 (2011–12, 2012–13). Cumulatively, we surveyed predator occurrences over 2790 camera-weeks from 154 camera sites (KC = 89 sites, WW = 65 sites). All winter camera sites were baited with frozen beaver carcasses to increase probability of detection ([MacKenzie et al., 2017](#)); $\text{pr}(\text{detecting wolverine} \mid \text{wolverine is present})$ approached 1.0 after 3 months of sampling ([Fisher and Bradbury, 2014](#)).

We subset only those sampling sites where either wolverine, grey wolf, cougar, coyote, red fox, or lynx were detected; that is we limited our state space $S = \text{wolverines} > 0 \mid \text{coyotes} > 0 \mid \text{cougar} > 0 \mid \text{fox} > 0 \mid \text{wolves} > 0$. This allowed us to explain variability in wolverine spatio-temporal distribution by those syntopic species where their ranges overlap ($n = 89$). Regression model β coefficients are derived as conditional probabilities within the data range of this state space. This limits our inference space to landscapes wherein at least one of these species occurs (analysis without subsetting is in Supplementary Information for comparison).

2.3. Habitat and carnivore covariates

Given existing knowledge of wolverine habitat selection ([Fisher et al., 2013](#); [Heim et al., 2017](#)), we modelled wolverine occurrence against natural land cover and abiotic features to build our core model, and then added anthropogenic disturbance features and occurrence of other carnivores to test our hypotheses. A species' realized distribution in space will be a function of habitat selection and interspecific interactions; by partialling variance due to landcover features we seek the additive effect of syntopic species. However we also recognize that current spatial distribution is to some degree influenced by past competition with heterospecifics, which we cannot parse out.

Natural land cover features were derived from LandSat satellite imagery and combined with a digital elevation model (DEM) to automate identification of 16 land cover types ([McDermid et al., 2009](#)). We focused on the five ecologically-relevant land cover types as supported by previous studies ([Heim, 2015](#); [Heim et al., 2017](#)): coniferous forest, mixed forest, deciduous forest, herbaceous cover and shrub cover. Each was measured as the proportion of land cover type within a 5000-m buffer around every camera site; this spatial scale was identified in a multi-scale analysis as best explaining variability of wolverine distribution ([Fisher et al., 2011](#)). We included two abiotic factors: persistent spring snow cover (hereafter, “snow cover”) and ruggedness. Snow cover was quantified as the percent area covered by persistent snow—the total number of years with snow out of 12 years (following [Copeland et al., 2010](#)). Ruggedness was quantified using the terrain ruggedness index (TRI), defined as the overall change in elevation

between grid cells (Riley et al., 1999). Anthropogenic disturbance features were derived from Alberta Biodiversity Monitoring Institute (ABMI) Human Footprint Map V2.2. We categorized anthropogenic features into block features (cut blocks, mine sites, well pads) and linear features, including energy exploration “seismic” lines (Dabros et al., 2018), roads, and trails. We used variance inflation estimation and confirmed all retained landscape variables were not collinear, with VIF < 3 (Zuur et al., 2010). All variables were scaled (mean = 0, s.d. = 1) to facilitate comparison of effect sizes.

We parsed camera data into week-long periods so each week is assumed an independent observation. Within each week, one or more detections indicated a weekly presence (1), and no detections indicated a weekly absence (0), for each species. Thus, we measured the presence/absence of each carnivore within the same week at the same site, replicated across 2790 weeks of sampling across the 152 sites.

2.4. Statistical analysis

We used generalized linear mixed models (Bernoulli distribution, logistic link) in R statistical software (ver 3.4.1; R Core Development Team); camera site was the random effect (from which repeat weekly samples are taken) and weekly wolverine occurrence was the response variable. GLMMs are a common tool for analysis of species' distribution data where multiple observations are derived from a single site location, and the random effect of “Site” accounts for expected entrained correlation from repeat samples (Rhodes et al., 2009). Unlike occupancy models which assume (and estimate) some proportion of non-detections as false absences (MacKenzie et al., 2017) – an assumption sometimes problematic for mobile animals (Broadley et al., 2019; Neilson et al., 2018; Stewart et al., 2018) – this analysis assumes 0's in serial detection data are true absences reflecting movement out of the area. Hence each week is a Bernoulli trial with the proportion of repeated detections across weeks related to the animal's selection of a site, which varies with landscape features.

We evaluated support for each of our hypotheses by comparing Akaike's information criterion (AIC) scores of models corresponding to each hypothesis. AIC scores models' ability to explain variation in wolverine occurrence across sites with the fewest parameters (Burnham and Anderson, 2002). We used a hierarchical approach to model selection. We first accounted for the influence of natural landscape heterogeneity on wolverine habitat selection by building a core model (CM) that contained only the best-supported abiotic and natural features, as determined by lowest AIC score. We maintained covariates from the CM in all successive model selection. We weighed evidence for our seven hypotheses by building 24 candidate models, each model accounting for some combination of the five different carnivores and the two kinds of anthropogenic disturbances (Table 1). We compared AIC weights as evidentiary support for each hypothesis. We validated the top model using the DHARMA package in R to test for overdispersion and visualize the model residuals.

3. Results

Wolverines and coyotes were detected most frequently, but all carnivores were represented sufficiently for modelling: wolverine at 70 sites, 292 camera-weeks; wolves 27 sites, 47 weeks; cougar 27 sites, 50 weeks; coyote 74 sites, 237 weeks; red fox 50 sites, 102 weeks; and lynx 27 sites, 47 weeks (Supplementary Information).

Competition outweighed the effects of predation risk or facilitation for wolverine distribution, and was strongly linked to anthropogenic landscape features created by energy exploration and extraction. Wolverine occurrence in space and time was best explained by coyote occurrence at the same sites in the same weeks, and the strength of this relationship varied with density of linear disturbance features (Table 2, Table 3). Wolverine weekly occurrence decreased with increasing linear feature density (seismic lines, roads, and trails); across the sampling

Table 1

Hypotheses for drivers of weekly wolverine habitat selection and the corresponding models and model variables for testing each hypothesis.

Hypothesis	Model no.	Model variables added to core model	Description
Predation	1	WOLF + COUG	Wolf occurrence and cougar occurrence
	2	WOLF	Wolf occurrence
	3	COUG	Cougar occurrence
Competition	4	COY + FOX	Coyote occurrence and fox occurrence
	5	COY	Coyote occurrence
	6	FOX	Fox occurrence
Facilitation	7	LYNX	Lynx occurrence
Disturbance features	8	LINEAR + BLOCK	Proportion of linear features and proportion of block features
	9	BLOCK	Proportion of block features
	10	LINEAR	Proportion of linear features
Predation mediated by disturbance features	11	COUG * LINEAR + WOLF * LINEAR	Cougar occurrence interaction with proportion linear features, and wolf occurrence interaction with proportion linear features
	12	COUG * BLOCK + WOLF * BLOCK	Cougar occurrence interaction with proportion block features, and wolf occurrence interaction with proportion block features
	13	WOLF * LINEAR	Wolf occurrence interaction with linear features
	14	WOLF * BLOCK	Wolf occurrence interaction with block features
	15	COUG * LINEAR	Cougar occurrence interaction with linear features
	16	COUG * BLOCK	Cougar occurrence interaction with block features
	17	COY * LINEAR + FOX * LINEAR	Coyote occurrence interaction with proportion linear features, and fox occurrence interaction with proportion linear features
	18	COY * BLOCK + FOX * BLOCK	Coyote occurrence interaction with proportion block features, and fox occurrence interaction with proportion block features
Competition mediated by disturbance features	19	COY * LINEAR	Coyote occurrence interaction with linear features
	20	COY * BLOCK	Coyote occurrence interaction with block features
	21	FOX * LINEAR	Fox occurrence interaction with linear features
	22	FOX * BLOCK	Fox occurrence interaction with block features
Facilitation mediated by disturbance features	23	LYNX * BLOCK	Lynx occurrence interaction with block features
	24	LYNX * LINEAR	Lynx occurrence interaction with linear features

frame, wolverines segregated from coyotes. However, wolverine occurrence was more likely, and more variable, when and where coyotes were absent (Fig. 2). The interaction term reveals a key, contrasting detail: wolverine and coyote were more likely to co-occur at sites with higher proportions of linear features, with a large effect size (interaction term $\beta = 3.20$, $SE \pm 0.71$, $p < 0.001$, Table 3) (see right panel in Fig. 3). Although wolverine and coyote rarely overlapped ($n = 8$ sites), the probability of co-occurrence increased 3-fold with each unit increase in linear feature density.

The subset of sites with wolverine-coyote co-occurrences had

Table 2

Generalized linear mixed models (Bernoulli distribution, logistic link) representing hypotheses for drivers of weekly wolverine habitat selection and comparison of model strengths using Akaike's information criterion (AIC) values. Covariate names and models refer to Table 1: CM = core model; BLOCK = polygonal features such as forest harvest cut blocks, mine sites, and well pads; LINEAR = linear features including energy exploration seismic lines, roads, and trails.

Hypothesis	Model Covariates	Model Rank	AIC	Delta AIC	AIC weight
Core model (CM)	Snow cover	21	1373.953	119.01	0.00
Predation risk	CM + WOLF + COUG	22	1374.677	119.74	0.00
	CM + WOLF	23	1374.685	119.74	0.00
	CM + COUG	20	1373.896	118.95	0.00
Competition	CM + COY + FOX	24	1375.280	120.34	0.00
	CM + COY	25	1375.940	120.99	0.00
	CM + FOX	19	1373.281	118.34	0.00
Facilitation	CM + LYNX	12	1360.281	105.34	0.00
Disturbance features	CM + LINEAR + BLOCK	7	1270.606	15.66	0.00
	CM + BLOCK	11	1360.190	105.25	0.00
	CM + LINEAR	4	1268.906	13.96	0.00
Predation risk mediated by disturbance features	CM + COUG * LINEAR + WOLF * LINEAR	9	1272.245	17.30	0.00
	CM + COUG * BLOCK + WOLF * BLOCK	18	1364.182	109.24	0.00
	CM + WOLF * LINEAR	8	1272.142	17.19	0.00
	CM + WOLF * BLOCK	15	1362.442	107.50	0.00
	CM + COUG * LINEAR	5	1269.025	14.08	0.00
	CM + COUG * BLOCK	14	1361.875	106.93	0.00
Competition mediated by disturbance features	CM + COY * LINEAR + FOX * LINEAR	2	1256.276	1.33	0.28
	CM + COY * BLOCK + FOX * BLOCK	17	1363.606	108.66	0.00
	CM + COY * LINEAR	1	1254.943	0.0	0.54
	CM + COY * BLOCK	16	1363.333	108.39	0.00
	CM + FOX * LINEAR	6	1269.719	14.77	0.00
	CM + FOX * BLOCK	13	1360.405	105.46	0.00
Facilitation mediated by disturbance features	CM + LYNX * BLOCK	3	1257.224	2.28	0.17
	CM + LYNX * LINEAR	10	1347.857	92.91	0.00

Table 3

Estimated β -parameters for variables in best-supported model explaining weekly wolverine habitat selection.

Parameter	Estimate	SE	Pr(z)
Intercept	-5.288	0.444	<0.001
Persistent spring snow cover	0.145	0.204	0.478
Linear features	-4.103	0.492	<0.001
Coyote occurrence	1.527	0.548	0.005
Linear features: Coyote occurrence	3.199	0.711	<0.001

significantly higher proportions of linear features than sites where wolverines and coyotes segregated ($t = 2.848$, $df = 7.03$, $p = 0.025$) (Fig. 4). Weekly wolverine and coyote occurrence depended on the

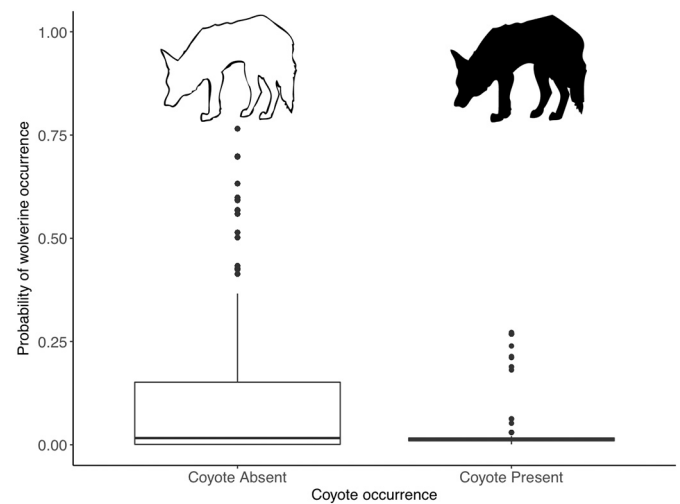


Fig. 2. Probability of wolverine occurrence as affected by coyote absence or presence within the same week in the Rocky Mountains ($n = 2790$ camera-weeks of observation across 152 camera sites).

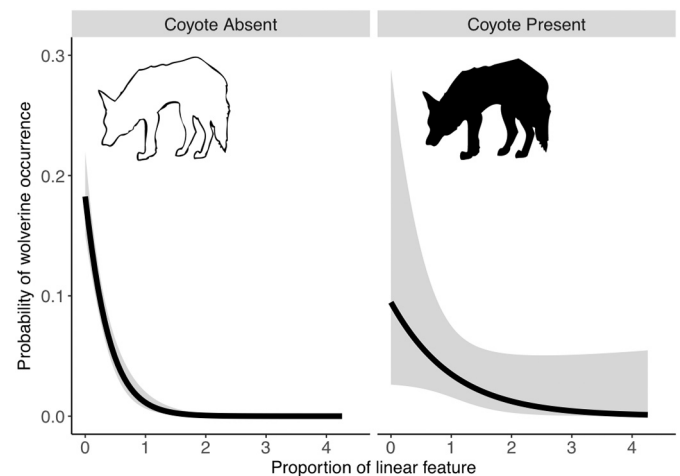


Fig. 3. Interaction term of best-supported model predicting weekly wolverine occurrence showing probability of wolverine occurrence as a function of proportion of linear features in the absence or presence of coyote in the same week ($n = 2790$ camera-weeks of observation across 152 camera sites). Wolverine were likely to co-occur with coyotes at sites with higher proportions of linear features.

degree of anthropogenic disturbance, wherein coyote tended to occur where linear proportions were high, and wolverine where linear proportions were low ($t = 21.79$, $df = 248.9$, $p < 0.001$) (Fig. 4).

Our core model, which included spring snow cover – a commonly cited wolverine habitat requirement (Copeland et al., 2010) – was not supported compared to the competition model ($AIC_w \sim 0.00$, Table 2). Likewise, there was no evidence that predation risk from wolves or cougars ($AIC_w \sim 0.00$, Table 2), or facilitation from lynx ($AIC_w \sim 0.00$, Table 2), explained wolverine spatiotemporal occurrence, compared with competition. Notably, competition alone did not best explain wolverine spatiotemporal occurrence compared with competition mediated by linear features ($AIC_w \sim 0.00$, Table 2). Interspecific interactions mediated by anthropogenic disturbance by coyotes ($AIC_w \sim 0.54$, Table 2) best explained spatiotemporal variability in wolverine occurrence, surpassing other abiotic or biotic models. The addition of red fox was an uninformative parameter (Arnold, 2010).

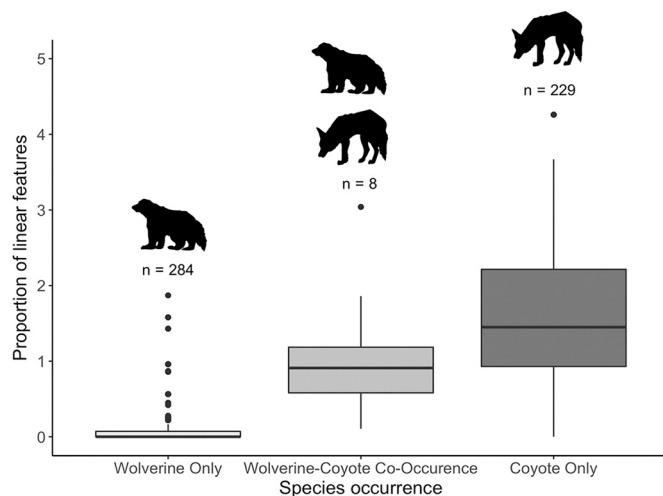


Fig. 4. Distribution of proportion of linear features at sites with species occurrences and co-occurrences, for wolverines and coyotes across both disturbed and undisturbed landscapes (n = the number of weeks of occurrences). Average proportion of linear features was significantly different between wolverine-only and coyote-only sites ($p < 0.001$), wolverine-only and wolverine-coyote co-occurrence sites ($p < 0.05$), and coyote-only and wolverine-coyote co-occurrence sites ($p < 0.10$).

4. Discussion

Competition with coyotes, not facilitation by lynx or predation by wolves and cougars, best explains wolverine distribution on the east slopes of the Canadian Cordillera. Rocky Mountain landscapes have been changing for a century (Fortin et al., 2019; Trant et al., 2020) and recently at unprecedented rates, and we show evidence that competition is a key driver of spatiotemporal wolverine distribution. The effect of this relationship eclipses abiotic factors such as availability of spring snow. Wolverines and coyotes were strongly segregated, suggesting syntopy (*same site at the same time*) was unlikely, despite sympatry (*overlapping ranges*). However the probability of syntopy increased threefold per unit increase in linear feature density such as seismic lines, roads, and trails, suggesting that disturbed landscapes facilitates opportunities for competition between wolverines and coyotes.

In complex landscapes the competitive advantage for sympatric species is determined by resource quality, availability, and accessibility; anthropogenic landscape change alters this competitive surface to the detriment of some species and the benefit of others. The decline of wolverines in this landscape (Fisher et al., 2013; Heim et al., 2017) and the success of coyotes – here (Heim et al., 2019) and across the continent in association with anthropogenic development (Hody and Kays, 2018) – suggests competition is favouring coyotes and contributing to wolverine declines. Wolverines and coyotes typically segregate on most undisturbed landscapes where wolverines occupy mountain terrain and coyotes, lowland terrain (Inman and Packila, 2015; Lofroth et al., 2007; Toweill and Anthony, 1988). However, coyote ranges have rapidly expanded due to increased exploitation of landscape disturbance, while the continental range of wolverines has contracted. Evidence shows that wolverines are receding from areas where spatial segregation from competitors was traditionally maintained, but are no longer capable of minimizing competition with coyotes. We contend this is due to enhanced connectivity for coyotes using linear features as movement subsidies. Linear features, such as roads and seismic lines, facilitate movement of predators into habitat that they traditionally would not occupy (DeMars and Boutin, 2018; Dickie et al., 2017). As linear features intersect deeper into wolverine habitat, evidence suggests they increase the probability of spatiotemporal contact between these two carnivores. Coyotes live at much higher densities than wolverines. Higher-density

species exploit resources at a much faster rate than low-density species, fully outcompeting them if intraspecific competition fails to compensate (Murrell and Law, 2003). We posit wolverine are out-competed through exploitation competition, wherein naturally low-density wolverines cannot compete with more numerically abundant coyote. If so the rapid expansion of coyotes has excluded wolverine from part of their range—which according to trapping records was occupied by wolverines until recent development (unpubl. data).

Coyote infiltration likely explains, in part, the avoidance of linear features by wolverine and their disappearance from disturbed landscapes with abundant coyotes (Fisher et al., 2013; Heim et al., 2017; Stewart et al., 2016). In boreal areas to the north where coyotes are much less abundant (Hody and Kays, 2018), wolverines actually do select for linear features (Scrafford et al., 2017), supporting our conclusions.

4.1. Caveats

We inferred types of interspecific interactions between carnivores using spatio-temporal co-occurrence as proxies for these interactions. This interpretation should be treated with caution as species co-occurrences do not always map to species interactions (Thurman et al., 2019). Here, we examined co-occurrence at the same locations, in the same week, of species exploiting the same resources; so we maintain spatiotemporal overlap reliably infers potential competition between wolverines and coyotes. In the truest definition, competition would indicate losses of fitness for wolverine in areas with high overlap with coyotes, and future research could focus on when and where wolverine fitness is impaired on disturbed landscapes, in relation to coyote density. Notably camera trap photos detected wolverines with kits in the Willmore Wilderness where coyotes were sparse, but kits were never observed in the Kananaskis Country where coyotes were abundant. Competition should be measured as the population outcomes of observed resource depletion, but over the vast spatial scales where competition outcomes manifest for large mammals this is logistically implausible, so we are left with inference from spatiotemporal occurrence as a guide. To reject this inference is to suggest these two species occupy the same space and time, but do not consume each other's very limited winter resources. Of course, this is a field study, and subject to the limitations inherent outside of a manipulated experiment.

Spatiotemporal co-occurrence is a novel approach to analyzing and characterizing interspecific interactions, which are typically challenged by logistical difficulties, though data collected using remote camera traps is opening new avenues for analysis of species interactions (see Tattersall et al., 2020a, 2020b; Frey et al., 2020). Our modelling approach assumes weeks are independent and that detection is perfect: zeros represent true absences from the site. Occupancy analyses (Fisher and Bradbury, 2014) support that assumption. Other approaches use two-species occupancy models (Erb et al., 2012; Mackenzie et al., 2004; Richmond et al., 2010) or incorporate a covariate measuring total detections at broader temporal scales (Fisher and Bradbury, 2014; Godsoe and Harmon, 2012; Wisz et al., 2013). These approaches measure the probability of occupancy based on total proportions of time spent at a site, rather than the probability of species co-occurrence explicitly within the same time frame. Our approach accounts for this explicit temporal co-occurrence by parsing data into weekly sampling units, which also enabled us to test specific hypotheses on interactions. This approach was especially helpful in characterizing how the different types of interspecific interactions were affected by landscape covariates, and was able to point toward the mechanism that might be driving behavioural changes within the carnivore community.

4.2. Conservation implications

Wolverine declines continue at this eastern edge of their range, a marked example of detrimental responses to anthropogenic landscape

change displayed by many northern mountain (Fisher et al., 2013; Heim et al., 2017) and boreal (Fisher and Burton, 2018; Wittische et al., 2021) carnivores. Range contractions signal the marked need for effective wolverine conservation, which necessarily targets the proximate mechanisms. Rather than attribute wolverine declines largely to climate, we offer evidence that landscape change is an ultimate, if not proximate, cause of declines in northern populations.

Declining distribution with increasing development is often ascribed to habitat loss (Brooks et al., 2002) but where the matrix is largely intact as in the Nearctic mountains, habitat abandonment *via* neophobia (Crane and Ferrari, 2017) is invoked. We posit rather than avoiding linear features *per se*, wolverines failed to successfully occupy areas with linear features as these entrain unsustainable competition *via* the coyotes that exploit them. Thus landscape management aimed at minimizing linear feature density, decommissioning roads and trails, and restoring linear features (Tattersall et al., 2020b) are likely needed to conserve wolverines in highly developed landscapes.

Anthropogenic disturbances are a principle factor in the global loss in biodiversity seen across terrestrial mammals (Butchart et al., 2010; Laliberte and Ripple, 2004). Landscape change can re-structure communities by altering the processes that traditionally sustained or prevented sympatry on heterogeneous landscapes. Resulting from – and perhaps synergistic with – climate change and landscape change, shifting competition surfaces may be an important factor shaping species distributions, potentially at the cost of population declines and range contractions, and landscape management in working landscapes – outside protected areas – needs to be a key part of conservation planning for northern carnivores.

CRedit authorship contribution statement

Gillian Chow-Fraser: Conceptualization, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – original draft. **Nicole Heim:** Data curation, Investigation, Writing – review & editing. **John Paczkowski:** Data curation, Investigation, Writing – review & editing. **John P. Volpe:** Methodology, Supervision, Writing – review & editing. **Jason T. Fisher:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, 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.

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Appendix A. Supplementary data

The summary of land cover similarities and differences across the study area (S1), summary of species detections (S2) and analysis of models from $S_{0,0}$ (S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author. Supplementary data to this article can be found online at doi:10.1016/j.biocon.2021.109435.

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