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RESEARCH ARTICLE

Carnivore community response to anthropogenic landscape change: species-specificity foils generalizations

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Abstract

Context Human exploitation of landscapes result in widespread species range loss and spatial community redistribution. Reduced species occupancy for large ranging terrestrial carnivore communities in disturbed or fragmented landscapes is a common outcome but the underlying mechanisms are ambiguous and the complexity of interacting mechanisms often under-appreciated.

Objectives To examine for similarity in spatial responses of carnivores to human-mediated landscape disturbance, we hypothesize common mechanism(s) to manifest at the community-level. To then incorporate a competitive surface, we evaluate the relative role interspecific interactions may play, where some species are benefited by altered habitat conditions.

Methods We deployed camera-trap arrays across a systematic grid-based study design to quantify carnivore occurrence. We tested hypotheses to understand spatial patterns of carnivore occurrence, in relation to biophysical and anthropogenic landscape factors, using multivariate analysis and species distribution models under an information-theoretic approach.

Results Differential response was found within the carnivore community, with some species occurring more frequently in disturbed landscapes while others displayed landscape scale avoidance of more highly disturbed areas. Interspecific interactions played an additive role to human-mediated response by some carnivores—suggesting generalist, human-adapted species, exaggerate interference interactions for other more sensitive species.

Conclusions Generalizable patterns are highly sought as clues to consistent mechanisms effecting changes to spatial distributions, but evidence weighs heavily in favour of species-specificity in responses implicating mechanisms that likewise vary for each species. Our findings underscore the value of a trait-based and community-level approach to

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understanding and managing the effects of anthropogenic land-use change on vertebrate biodiversity.

Keywords Anthropogenic disturbance · Carnivore · Community composition · Occupancy · Spatial distribution · Generalist · Conservation

Introduction

Human footprint and habitat disturbance are primary threats to biological diversity across taxonomic communities worldwide (Sanderson et al. 2002; Leu 2008; Ewers et al. 2013). Range reductions and population declines are particularly notable for communities of large mammalian carnivores (Gittleman 2001) exhibiting high dispersal rates, low population density, low fecundity, and requiring expansive intact home ranges (Crooks 2002; Watts and Handley 2010). Ecologists seek repeating patterns consistent among species and systems as evidence of common mechanisms underpinning ecological generalities (Lawton 1999; Turchin 2001). However, although species loss and population reductions are often the result of the ever-increasing impacts of human occupation and exploitation of natural landscapes (Brooks et al. 2006; Díaz et al. 2006; Cardinale et al. 2012; Hooper et al. 2012), spatial responses to anthropogenic landscape change have as yet to reveal commonalities among sympatric vertebrate communities. A uniform response to increasing human habitat disturbance across all species of a carnivore community may be a logical prediction, but the direction and magnitude of community-level response may also depend on individual species' traits and ability to balance resource acquisition, competition, and mortality risk (Bowne and Bowers 2004; Mittlebach 2012). For specialist carnivores or those sensitive to landscape change, the ecological mechanisms being altered—loss of foraging, increased risk—may dictate each species' spatial response, predicted as a net loss. For some generalist carnivores, exploitation of human dominated landscapes can manifest as behaviorally-mediated shifts in spatial and temporal habitat use (Tigas et al. 2002; Virgós 2002; Markovchick-Nicholls et al. 2008)—a net gain. Moreover, any significant reduction of apex, or dominant, carnivores can lead to top-down trophic cascades—releasing subdominant carnivore abundance and expanding the spatial range of such species more resilient to anthropogenic disturbance (Caro and Stoner 2003; Fortin et al. 2005; Wirsing et al. 2007; Beschta and Ripple 2009). Species-specific responses to landscape change manifests "winners and losers" (Fisher and Burton 2018; Farr et al. 2019), with net gains in functional response for some carnivores (e.g. coyote, raccoon) and net losses for others (e.g. Grizzly bear, wolverine). Reducing carnivore communities to only those species most resilient to human-mediated landscape changes is a significant conservation concern. Contemporary evidence worldwide shows a diverse community of carnivores is needed to maintain ecosystem stability, thereby strengthening resilience to the negative effects of top-down trophic cascades (Ritchie and Johnson 2009; Estes et al. 2011; Ripple et al. 2014). While predator–prey interactions have long been examined (Lotka 1925), recent attention has moved to better understanding predator–predator interactions (Palomares and Caro 1999; Linnell and Strand 2000; Ritchie and Johnson 2009) and accounting for the functional role that interspecific interactions—interactions that include habitat enrichment, mutualism, predation, and competition—play within these communities (Soulé et al. 2003). Unlike predator–prey interactions which are a function of direct or anticipatory consumption of one species by another, top predators in a community—defined by their position at or near the top of the food web (Sergio et al. 2014)—can limit population abundance of smaller 'meso-predators' through direct predation or indirect competitive interactions over vital resources (Glen and Dickman 2005; Ritchie and Johnson 2009). The reduction or removal of a top predator liberates meso-predators from interference interactions—the "meso-predator release hypothesis" (Litvaitis and Villafuerte 1996; Crooks and Soulé 1999; Gehrt and Clark 2003; Prugh et al. 2009). Increase in relative abundance of one, or more, can further cascade to limit niche space for rarer species with more specialized traits (Amarasekare 2003; Murrell and Law 2003; Ordeñana et al. 2010)—a process described under competition-colonization trade-off model (Levins and Culver 1971). Regardless of environmental variables and resource supply, the presence of a competitor reduces habitat profitability and may thereby drive shifts in spatial distribution among a competitive carnivore community (Godsoe and Harmon 2012;

Fisher et al. 2013a; Lindenmayer et al. 2014). Human disturbance that influences resource acquisition and habitat security may indirectly increase the competitive landscape for wildlife communities' at large spatial scales, relegating subdominant species to less suitable habitat, or result in the extirpation of some species from a particular region (Putman 1994; Amarasekare 2003; Wiens and Moss 2005). Unfortunately, species interactions of these types are exceedingly difficult to measure in the wild. We can however measure spatial distributions as outcomes of these processes, under the assumption that the extent of landscape disturbance on species and their interactions may be evident in spatial distribution—including co-occurrence and segregation of sympatric carnivore communities. As much as ecologists are eager for ecological generalities (Lawton 1999; Turchin 2001), we predict patterns of spatial segregation—or differential space use—among sympatric carnivores are likely context and species dependent, changing with community membership and landscape characteristics.

Here we test the hypothesis that species within a native community located in the northern Rocky Mountains exhibit a similar spatial response to various forms of disturbance; or alternatively, if species exhibit a differential spatial response to disturbance, favouring some while hindering others. In addition, we test the hypothesis that the distribution of heterospecific predators additionally influences distribution, as an indirect outcome of disturbance—using the term "interspecific interactions" as shorthand for the *outcomes* of species interactions. We ask: (1) Is there significant spatial dissimilarity among carnivores (measured by species occurrence) in response to anthropogenic landscape factors? (2) Do interspecific interactions play a consistent and significant role in explaining carnivore occurrence patterns, additive to biophysical heterogeneity and anthropogenic factors? We predicted carnivore community composition would shift as a function of anthropogenic disturbance, in three ways: (1) top predators would decrease with increasing anthropogenic landscape change, regardless of source (petroleum, transportation, forest harvesting); (2) meso-predator species would increase with increasing anthropogenic landscape change; (3) interspecific interactions among competing carnivores affect species distributions, additive to the effects of anthropogenic factors. If we can identify common spatial responses by sympatric carnivores to different forms of land-use features, inferences about common mechanisms follow—those that are key to identifying generalities in species' response to anthropogenic change.

Methods

Study area

We surveyed nine carnivore species within the Front Ranges of the Canadian Rocky Mountains spanning 15,000 km^2 the complex of Banff, Yoho, and Kootenay National Parks and the provincially managed region of Kananaskis Country (Fig. 1). Land use activities within the National Parks complex are spatially restricted to a large bisecting highway, recreational trails, lease areas, and two town sites. Human activities are limited to highway transportation, non-motorized recreational hiking, biking, skiing and camping. We group the provincially managed areas into the Kananaskis Country region, wherein legally designated Park and Public Land Use Zones are managed according to various land designations supporting conservation, recreation and industry. Recreation is restricted to non-motorized activities in Ecological Reserves while designated non-motorized activities may be permitted in the Provincial Parks. Commercial activities are permitted within a series of Public Land Use Zones located within the more eastern areas of the Kananaskis Region (e.g. oil and gas exploration, timber harvest). Both the National Parks complex (NPC) and the Kananaskis Country (KC) region are dominated by alpine and subalpine natural subregions, with areas of Montane subregion at lower elevations. KC transitions from Alpine and Subalpine into Montane and is bordered to the east by Foothills Parkland. Topography across the area is rugged, spanning an elevation gradient from 825 m to above 3600 m. The study area is home to a native suite of medium- to large-sized mammalian carnivore species that include Grizzly and Black bear (*Ursus arctos* and *U. americanus*), cougar (*Puma concolor*), Canada lynx (*Lynx canadensis*), bobcat (*Lynx rufus*), wolf (*Canus lupus*), coyote (*Canis latrans*), fox (*Vulpes vulpes*), and wolverine *(Gulo gulo)* and marten *(Martes americana)*. This study area represents a mosaic of mountain topography with varying

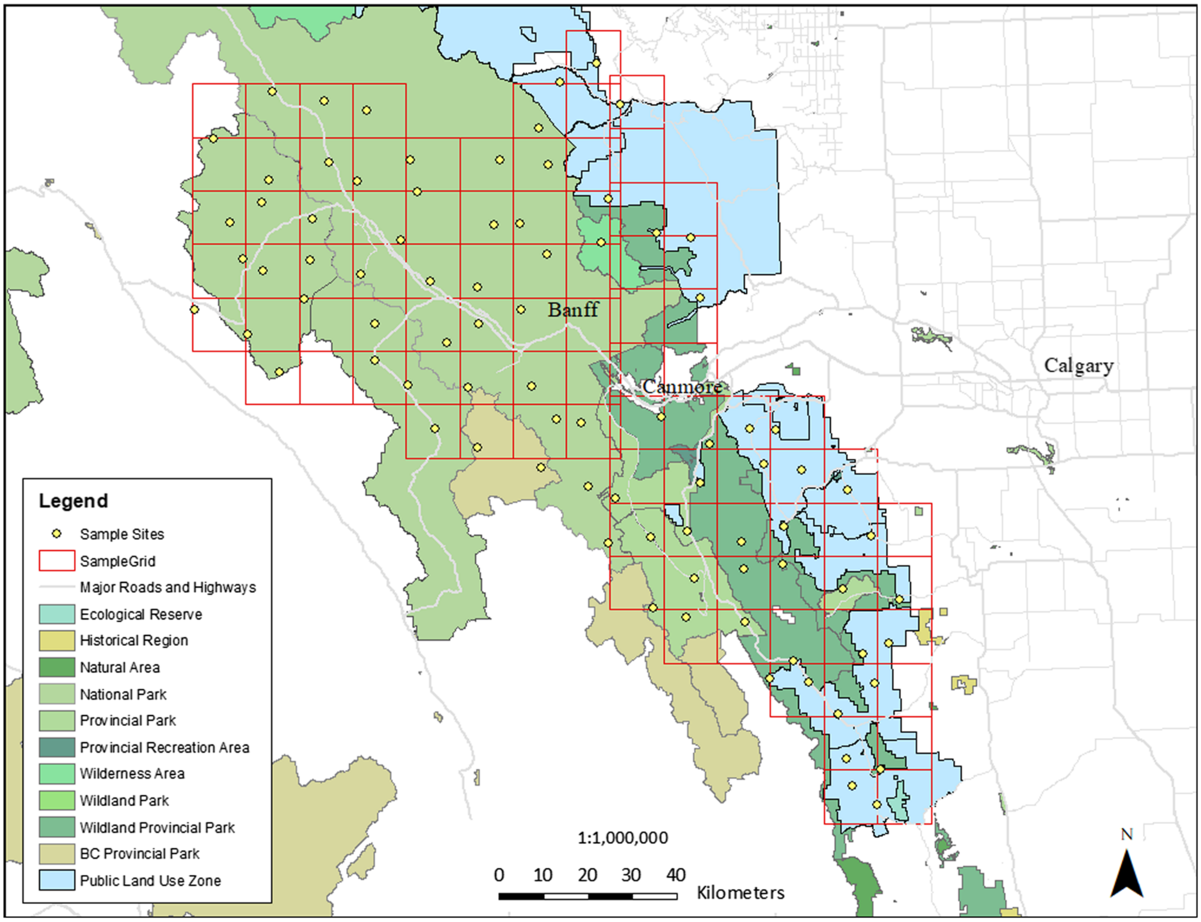

Fig. 1 Study area map. The systematic 12 × 12 km^2 grid-based study design (red grid cells) and distributed site locations (yellow points) spanned the northern region of the Rocky Mountains, a region encompassing a National Parks Complex, Kananaskis Country, and Alberta's east slopes. (Color figure online)

degrees of landscape protection and density of human land-use activities. Forest loss within the eastern ranges of the study area has been extremely rapid and expanding due to industrial development. Timber harvest is a long-standing dominant development pressure on the landscape within and east of the Kananaskis Country region, with increases in oil and gas exploration over time. Resulting forest loss along the Rocky Mountain East Slopes of Alberta shows per area rates of loss rivalling many in the Americas, showing a rate of nearly 7 percent deforestation in only 12 years on lands outside of protected areas (Global Forest Watch Canada 2014). Although we expect the carnivore community has responded to past disturbance, ours is the first examination of the entire community in the disturbed slopes of the Rocky Mountains, and hence examines contemporary relationships.

Study design

We employed a 12 × 12 km^2 (144 km^2) systematic grid-based sampling design (Fig. 1), across an area approximately 15,000 km^2 within the grain size of grid cells emulating a female wolverine home range size (Koen 2008), the most wide-ranging of our study species. We subjectively placed one sampling site within each of 91 grid cells based on topography (to maximize probability of detection) and access, consistent with multiple previous studies (Burton et al. 2011; Fisher et al. 2013b; Konstant et al. 2015).

Independence among sample sites was facilitated by an approximate minimum distance of 6000 m.

Species sampling

We quantified carnivore occurrence using infrared remote camera (IRC) traps (Thompson 2004; Long et al. 2008; O'Connell et al. 2011). At each site we deployed IRC traps (Reconyx, Holmen, Wisconsin, USA) positioned facing a tree baited with a beaver carcass and 30 mL of scent lure (O'Gorman's Co., Montana, USA). Cameras were programmed at high sensitivity, five images per trigger, 1 s apart, and rapid fire with no delay. Sampling and rebaiting occurred on a monthly basis through January–April (2012). Sampling seasonality limited species detected to exclude bear species during winter hibernation period. Our study area was a polygon around the outermost cameras in the array, while a sampling site was defined as the area around the trap potentially imaged by the camera (Burton et al. 2011). Digital photographs were classified to quantify occurrence and summarised into two response metrics: serial monthly detection data (1 = detection; 0 = non-detection) and an index of use across three months (0–3). These data did not account for unique individuals and focused on generating indices of use. The resulting data frame consisted of n = 91 sites, surveyed t = 3 times.

Analyses

Estimating occupancy over space

Modelling serial occurrence data, such as repeated detections via camera traps, is an area of active research without current consensus (Rota et al. 2009; Banks-Leite et al. 2014; Stewart et al. 2018). Instead of investing in a single modelling approach and its assumptions, we analysed camera data using different approaches and sought convergence in interpreting results. First, serial detection data were used to estimate probability of occupancy (ψ) and probability of detecting a species (p) if present (MacKenzie 2006; Royle 2006; Fisher and Bradbury 2014) accounting for imperfect detection. We then modelled species spatial distributions against landscape covariates using a form of constrained ordination (redundancy analysis) and species distribution modelling (generalized linear models), which assume that the occurrence or persistence of a species at a site is related to the landscape within some defined area around that site (Guisan and Thuiller 2005).

Quantifying biophysical and anthropogenic covariates

In ArcGIS 9.3.1 (ESRI, Inc.), we quantified biophysical and anthropogenic landscape covariates around each camera site. We imposed circular buffers of 2500-m radius around each sampling point (Fisher et al. 2011). Expecting that carnivore distribution was, in part, explained by natural landscape heterogeneity, we quantified landcover from a 16-class landcover dataset based on LandSat imagery and a digital elevation model (DEM) (McDermid et al. 2009). We predicted carnivore distribution is also a function of topography and snow cover in this highly rugged landscape. We calculate terrain ruggedness using the topographic ruggedness index (Riley et al. 1999) based on a 25-m moving window within the 2500-m radius buffer. We quantified years (12) of persistent spring snow covering a temporal buffer between April 14 and May 15 using Moderate Resolution Imaging Spectroradiometer (MODIS) satellite data (Hall and Riggs 2007; Copeland et al. 2010). Persistent spring snow can be used as a surrogate for annual snow pack found to influence space use patterns for species better adapted to travelling across deep snow, such as lynx and wolverine, or species less adapted to deep soft snow packs shown by smaller-footed canids (Seip 1992; Muray and Larivière 2002; Brodie and Post 2010). Predicting that anthropogenic footprint would alter carnivore distribution, we quantified the percent area of existing anthropogenic landscape footprint features (ABMI 2010) in 12 composite classes: % area of block features (urban or industrial disturbance), and density (km/km^2) of linear features (roads, cutlines, pipelines, seismic lines, motorized and non-motorized recreational trails). All landscape classification herein are derived from these data products and represent a contemporary landscape which is, of course, the result of past disturbance as well. What we define as "natural features" also includes regeneration from past disturbance (such as fire, possibly anthropogenic), but we distinguish "anthropogenic features" as those of contemporary origin.

Table 1 All RDA model output and RDA model variation explained by each model tested using redundancy analysis using an F-statistic with a significant level of 0.001

Model no.	Matrix sets	No. of var.	Total inertia	Constrained proportion	Unconstrained proportion	R^2	R^2 (adj)	df	F	Pr(> F)
1, global	All species + all covariates	22	0.4939	0.2969	0.7031	0.30	0.18	13	2.50	0.005
2	All species + anthropogenic	12	0.4939	0.1128	0.8872	0.11	0.07	4	2.73	0.005
3	All species + biophysical	18	0.4939	0.2777	0.7223	0.28	0.20	9	3.46	0.005
4	Sensitive + anthropogenic	7	0.3183	0.0955	0.9044	0.10	0.05	4	2.27	0.015
5	Tolerant + anthropogenic	9	0.4766	0.0935	0.9064	0.09	0.05	4	2.22	0.004
6	Mega + all covariates	18	0.5266	0.3440	0.6560	0.34	0.23	13	3.11	0.001
7	Meso + all covariates	18	0.3695	0.2305	0.7695	0.23	0.10	13	1.77	0.007
8	Mega + anthropogenic	8	0.5266	0.1606	0.8394	0.16	0.12	4	4.11	0.002
9	Meso + anthropogenic	8	0.3695	0.0661	0.9338	0.07	0.02	4	1.52	0.131
10	**Mega + biophysical**	**14**	**0.5266**	**0.3879**	**0.6121**	**0.39**	**0.32**	**9**	**5.70**	**0.001**
11	Meso + biophysical	14	0.3695	0.1522	0.8478	0.15	0.06	9	1.62	0.033

Model 10, highlighted in bold shows most variation explained by constrained, or measured, explanatory variables

We estimated the relative effect of heterospecific occurrence on carnivore distribution by modelling monthly frequency of use (0–3) by other carnivores. We standardized ($X - \mu/\sigma$) independent variables to compare effect sizes, tested for multicollinearity using Pearson correlation coefficient (r^2) matrices and multi-panel scatterplots and used variance inflation factor (VIF) estimation to identify collinear variables (Zuur et al. 2013). Following a stepwise approach, we retained variables with $VIF < 5$ (see Appendix S1, Supplementary Material). Conservative collinearity analysis and variable reduction minimized bias that may result from high levels of correlation between vegetation land cover and existing human footprint features.

Testing for dissimilarity in response

Ordination

We tested our prediction that carnivore species respond dissimilarly to anthropogenic landscape change—irrespective of biophysical features—using redundancy analysis (RDA). RDA is a multivariate method of constrained ordination that evaluates similarity in response and can therefore be used to test the inverse, revealing dissimilarity in response by deviation in model strength and direction (McCune et al. 2002). We modeled species occurrence indices (0–3) as the response matrix against the set of explanatory variables. To reduce model complexity and increase partitioning of variance, response and explanatory matrices were ordinated by subsets. Response matrices were grouped according to species predicted sensitivity to human disturbance and body size. Explanatory matrices were separated by biophysical and anthropogenic landscape factors. We specified 11 RDA models hypothesized to be most ecologically important for the carnivore community under investigation (Table 1).

We assigned low weight to rare species using a Hellinger transformation (Legendre and Gallagher 2001), accounting for a disproportionate number of zeros inherent in carnivore occurrence data. We compared the relative strength of model fit, or the amount of variation explained, by calculating the r^2 and adjusted r^2 value using Ezekiel's formula (Borcard et al. 2011). We report the total variation explained by each model, the proportion of variance explained in the data for the constrained (measured) variables, the unconstrained (unmeasured) variables, and by the first two canonical axes for each model. Using a significance level of 0.001, the null hypothesis being tested is that there is no (linear) relationship between the response data matrix and the explanatory data matrix (Borcard et al. 2011). Therefore, a relatively higher

F-statistic (> 1) with a significance value (Pr(> F)) at or below 0.001 suggests that there may be a significant relationship between the response and explanatory variables included in the specified model. We plotted point-vector biplots to interpret the strength and direction of associations and to examine the similarity among species occurrence patterns in ordination space and in relation to explanatory variables, indicated by the length and angle of vectors relative to the axes. With the greatest amount of variation explained by the first two axes, we examined biplots representing scaling of species for axis 1 (RDA 1) and axis 2 (RDA 2).

Species distribution models

We used species distribution models (SDM) to examine each carnivore species' occurrence relative to landscape factors—as well as evaluate the relative role of interspecific interactions, additive to landscape factors. We modelled hypotheses about the relative roles of anthropogenic features in explaining carnivore distribution against natural landcover, topography, snow, and heterospecifics. We used generalized linear models (binomial errors, log link) in R version 3.0.2 (R Core Team 2014), with serial detection data (0,1) over three survey periods for each survey location modelled against all independent variables (Table 1). Explanatory variables were grouped within four candidate model sets: landcover, topography, climate and anthropogenic landscape change (see Appendix S3, Supplementary Material). Over multiple species it is challenging to create a priori hypotheses to predict the variables that best explain species-specific occurrence over space; instead we used a stepwise progression of model simplification to select the best-fit, or minimum adequate, model (Crawley 2007) for each model set. Using an information-theoretic approach, we compared Akaike Information Criterion (AIC) scores within and across model sets (Anderson 2008), ranking models using differences in AIC values (ΔAIC) and weight of evidence (AICw). We added the occurrence (0, 1) of a heterospecific to the parameters retained in each minimum adequate, or best-fit model, across the four candidate model sets for each species (Table 2). Model weight was then compared to those without the inclusion of the heterospecific to infer the relative influence of interspecific interactions with landscape factors. Possible violation of assumptions or model misspecification were investigated by examining model residuals and diagnostic plots (Zuur et al. 2010; Matthiopoulos 2011). Cleveland plots were used to examine for outliers and all measured covariates were standardized to a common scale that allows for comparison of parameter effect size (Zuur et al. 2010). The β parameters for all variables included in best-fit models were reported in Appendix S2, Supplementary Material.

Results

Spatial patterns of occupancy

Across 91 sites and 3 monthly survey periods, we detected carnivore species on 7500 occasions.

The proportion of occurrence varied with species. Wolverine and marten made up > 50% of the species detections (30.13% and 24.25% respectively), followed by coyote (13.07%), lynx (8.55%), red fox (8.28%), wolf (6.16%), bobcat (5.33%), and cougar (4.24%). As hypothesized, the spatial pattern of occurrence varied by species and with increasing anthropogenic footprint along the west–east gradient (Fig. 2). The probability of cougar, red fox, and wolf occurrence increased marginally to the east, while bobcat displayed a sharp peak. Lynx and marten increased westward. Coyote was the only species to show a marked increase with increasing disturbance; conversely, wolverine showed a marked decrease outside of the National Parks complex and into the more developed Kananaskis Region.

Dissimilarity in carnivore community response

Ordination

The carnivore community did not respond similarly to biophysical or anthropogenic landscape factors. The global RDA model (model 1), which incorporated all independent variables (Table 1), only explained 49% of the total variation (total inertia = 49%, Table 1), with as little as 29.69% of the variation explained by the constrained (measured) explanatory variables. Therefore, 70.31% of the variation in the data was explained by the unconstrained, or unmeasured, variables not included in our comprehensive model. The point-vector bi-plot for RDA model 1 shows most

Table 2 All single-species distribution model selection for each carnivore species detected within the regional study area

Species	Model	Model variable	Direction of association (+/−)	AIC	ΔAIC	AICw
Fox	Landcover	HERB	+	99.99	0.00	0.51
	Topography	TRI	+	104.59	4.60	0.05
	Climate	SP.SNOW	–	104.17	4.18	0.06
	Human footprint	LINROAD	–	101.92	1.93	0.19
	Landcover + coyote	HERB + COYOTE	+, −	101.97	1.98	0.19
Coyote	Landcover	DENSE + OPEN + SHRUB + REGEN + BARE	−, +, −, +, −	96.04	6.28	0.03
	Topography	TRI	–	108.57	18.81	0.00
	Climate	SP.SNOW	–	97.33	7.57	0.02
	Human footprint	LININD	–	89.76	0.00	0.69
	Human footprint + wolf	LININD + WOLF	−, −	91.72	1.96	0.26
Bobcat	Landcover	DENSE + MODERATE + SHRUB + HERB	−, −, −, +	60.93	0.58	0.37
	Topography	TRI	+	66.84	6.49	0.02
	Climate	SP.SNOW	+	65.13	4.78	0.05
	Human footprint	LINROAD + LINREC	−, +	64.64	4.29	0.06
	Landcover + coyote	DENSE + MODERATE + SHRUB + HERB + COYOTE	−, −, −, +, +	60.35	0.00	0.50
Lynx	Landcover	DENSE + MODERATE + HERB	+, +, +	97.94	10.20	0.01
	Topography	TRI	+	98.97	11.23	0.00
	Climate	SP.SNOW	+	98.80	11.06	0.00
	Human Footprint	INTERCEPT	–	98.85	11.11	0.00
	Landcover + cougar	DENSE + MODERATE + HERB + WOLF	+, +, +, −	87.74	0.00	0.98
Cougar	Landcover	DENSE + MODERATE + BARE	+, +, +	68.09	0.35	0.39
	Topography	TRI	+	74.20	6.46	0.02
	Climate	SP.SNOW	–	72.29	4.55	0.05
	Human footprint	BLOCKURB	+	71.43	3.69	0.07
	Landcover + wolf	DENSE + MODERATE + BARE + WOLF	+, +, +, +	67.74	0.00	0.47
Wolf	Landcover	BARE	–	94.51	14.51	0.00
	Topography	TRI	–	85.01	5.01	0.06
	Climate	SP.SNOW	–	80.00	0.00	0.68
	Human footprint	LININD	+	94.44	14.44	0.00
	Climate + coyote	SP.SNOW + COYOTE	−, −	81.87	1.87	0.27
Marten	Landcover	DENSE + MIXED + SHRUB + BARE	+, +, +, +	84.82	9.28	0.01

Table 2 continued

Species	Model	Model variable	Direction of association (+/−)	AIC	ΔAIC	AICw
	Topography	TRI	+	87.18	11.64	0.00
	Climate	SP.SNOW	+	88.63	13.09	0.00
	Human footprint	LININD	−	84.27	8.73	0.01
	Human footprint + coyote	LININD + COYOTE	−, −	75.54	0.00	0.97
Wolverine	Landcover	DENSE + MIXED + SHRUB + HERB + REGEN + SNOW.ICE	+, −, +, +, −, +	213.78	4.42	0.10
	Topography	TRI	+	273.27	63.91	0.00
	Climate	SP.SNOW	+	231.17	21.81	0.00
	Human footprint	LININD	−	221.96	12.60	0.00
	Landcover + coyote	DENSE + MIXED + SHRUB + HERB + REGEN + SNOW.ICE + LININD + COYOTE	+, −, +, +, −, +, −, −	209.36	0.00	0.90

Models were ranked using AIC, Akaike Information Criterion. The best-fit model set is indicated by ΔAIC = 0 and AIC weight = 1.00

carnivore species to cluster in ordination space along axis 1 in relation to a combination of biophysical and anthropogenic covariates (Fig. 3), but with poor strength of association (adj. $r^2 = 0.178$, $Pr(> F) = 0.005$) (Table 1). Though model strength was modest, all models consistently showed a species-specific response to the combination of anthropogenic covariates, varying by magnitude and direction in ordination space (Fig. 3). Where bobcat was most closely and positively associated with urban block features, cougar and fox were positively associated with linear recreational trails, wolf positively associated with roads, and lynx with regenerating forest cover. The strongest pattern of dissimilarity in response was found between wolverine and coyote. Wolverine was situated on the negative end of axis 1 having positive associations with three landcover types (dense conifer, shrub, snow and ice) and adversely associated to all anthropogenic covariates. In contrast to wolverine, coyote was situated on the positive side of axis 1 and was strongly associated with increased density of linear industrial features (Fig. 3).

Though RDA results presented poor model strength, ordination did show a consistent dissimilarity in response within the carnivore community, regardless of their groupings and across all models tested (Table 1). Most notably, a single prevailing pattern revealed the high degree of dissimilarity in response between occurrence of wolverine and coyote.

Species distribution models

Supporting RDA modelling results, each carnivore species responded differently to biophysical and anthropogenic factors in their environment (Table 2). Felid (bobcat, lynx, and cougar) and fox distributions mostly strongly selected natural landcover variables. Wolves selected against persistent spring snow. Wolverine selected a combination of natural landcover, anthropogenic factors, snow cover, and heterospecific occurrence. Again, coyote and mustelid response were highly divergent: coyote positively selected for linear industrial features, whereas marten and wolverine negatively selected for these features. The inclusion of heterospecifics in the best-fit landscape model further improved model fit for the three felid species, marten and wolverine (Table 2). Conversely, the addition of heterospecifics did not improve model fit among the canids (fox, coyote, or

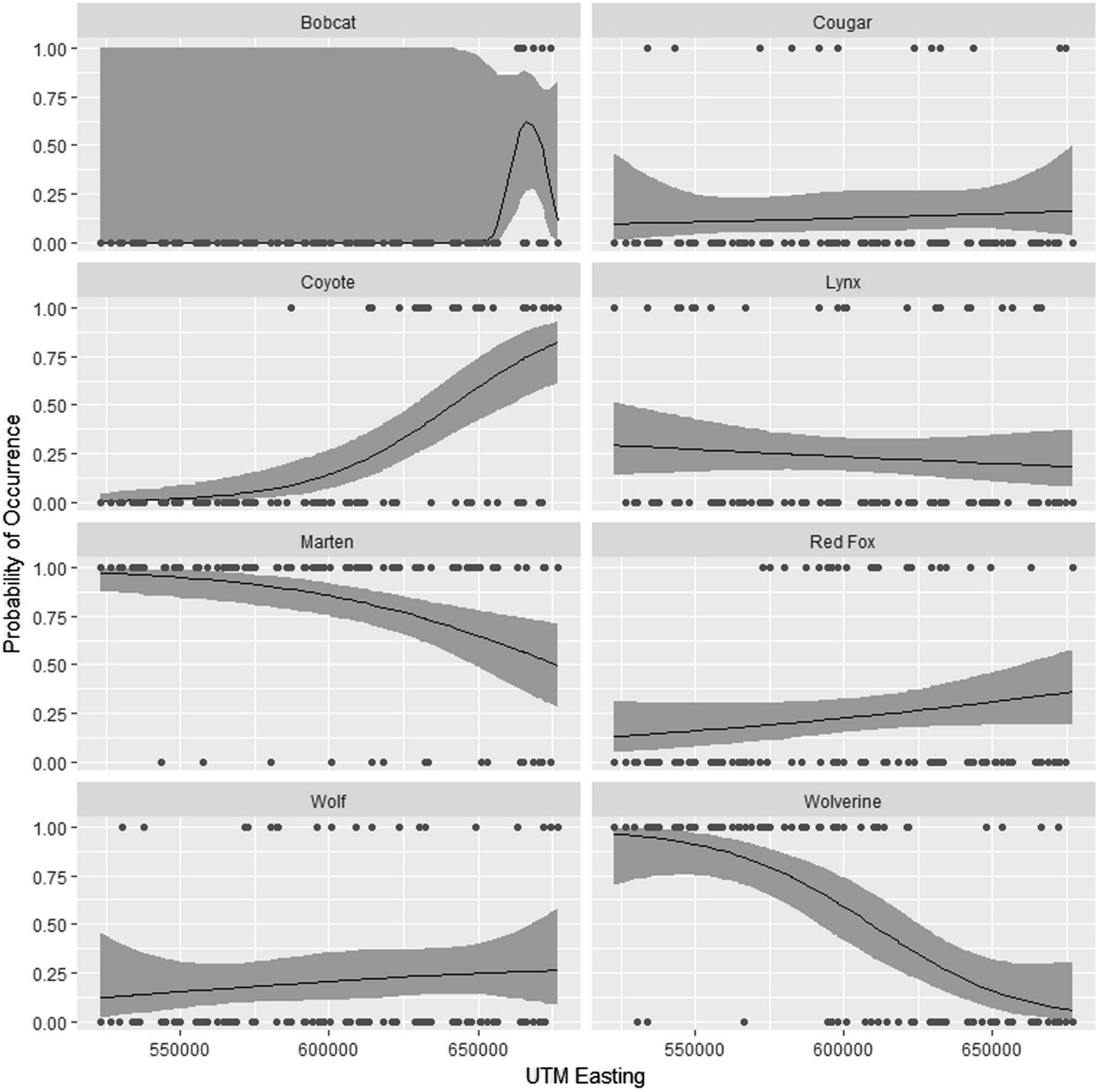

Fig. 2 Compares the probability of occurrence across space (UTM east coordinates, Map Datum: Nad 83, Zone 11) for each species modeled from the west boundary of the National Parks complex to the east boundary of the Kananaskis Region

wolf). For felids, mustelids and fox detected the inclusion of a coyote or wolf improved model fit, suggesting the probability of large-sized canid occurrence (coyote or wolf) may be additive to effects of biophysical and anthropogenic landscape factors driving spatial patterns within the carnivore community.

Discussion

As niche theory would predict, carnivore species varied in their response to landscape factors, making common mechanisms highly unlikely and obscuring the search for generalizations in species' spatial response to anthropogenic landscape change. Linear footprint (e.g. roads, seismic lines, and trails) is the most spatially extensive and pervasive form of

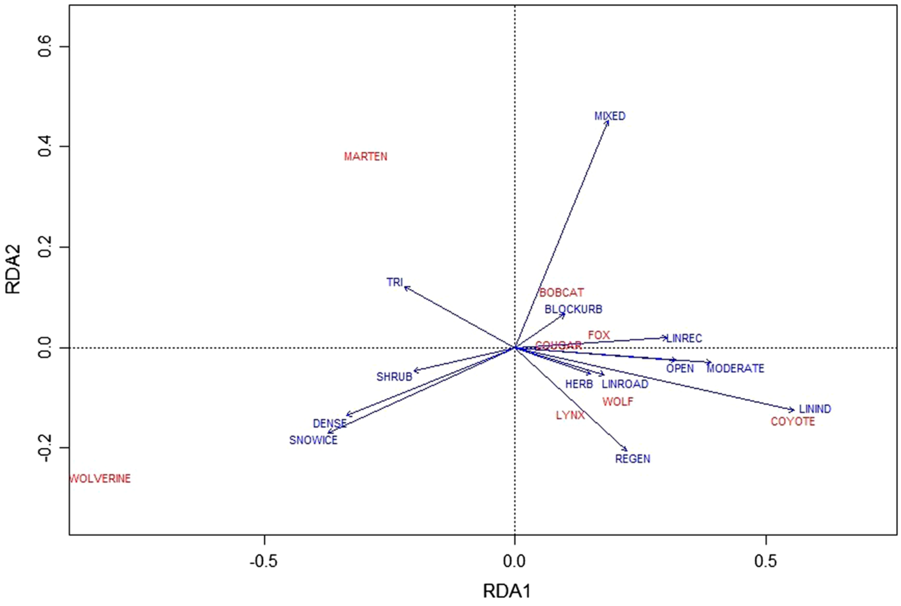

Fig. 3 Point vector biplot graphically represents the scaling of all carnivore species occurrence (response matrix) in ordination space in relation to all of the landscape variables (explanatory matrix) measured at the 2500 m scale. For interpretation, correlation strength is indicated by the length of the arrows and angle of vectors relative to the axes. Variable descriptions included in this plot can be found in Appendix 1, Supplementary Material

anthropogenic disturbance in this landscape. Although known to expedite travel for wolves and hence increased predation rates (McKenzie et al. 2012; Dickie et al. 2017) an observation one could logically extrapolate to other carnivores—linear footprint nonetheless did not widely explain variability in carnivore response and distribution. Instead, different anthropogenic features appeared to change different processes for different species, in different ways. This is what we expect from both niche theory, and from risk-reward theory (Smith and Smith 2001; Soberón 2007; Holt 2009). This greatly complicates both ecological inquiry and landscape management for biodiversity conservation, placing emphasis on mitigating cumulative effects of multiple features produced by multiple sectors—a worldwide conservation hurdle for the new millennium.

Our results also suggest impacts on the carnivore community in the northern Canadian Rocky Mountains are yet to be fully realized, with evidence that some species are "winning" and some are "losing" (Fisher and Burton 2018). If so, we might expect to see generality in species response to disturbance over time, expressed as changes to community-level shifts or reductions in spatial distribution. Mounting evidence suggests the threats of habitat loss and degradation on local communities are underestimated due to a temporal lag in population-level effects—extinction debt—a debt that is gradually paid over time as local extinctions are realized (Tilman et al. 1994). Though empirical studies are lacking, current knowledge suggests that long-lived species with low extinction and colonization rates—such as terrestrial carnivores—are more likely to experience delayed effects of recent disturbance, effects difficult to detect over short periods of time (Kuussaari et al. 2009). With rapid and significant resource extraction and associated landscape disturbance (Global Forest Watch Canada 2014), our challenge in uncovering similarity in response among carnivores may be rooted in a temporal lag. Additive to resource development, our protected areas networks are subject to a significant increase in spatial and temporal land use for recreation and the subsequent development pressure for diverse recreational opportunities—land-use activities often seen as relatively benign but can negatively impact diversity and community composition of carnivores (Reed and Merenlender 2008). The cumulative costs of industrial and recreational disturbance may not be evident until marked population declines are observed.

Conclusion

The seemingly disparate spatial distribution and response to anthropogenic disturbance between coyote and wolverine may be early evidence the east slopes of the Canada Rockies are indeed experiencing temporal lag effects of cumulative impacts. Past evidence (Heim et al. 2017) corroborate our findings, lending confidence to conclusions about these more data-depauperate species. Wolverine negatively respond to increasing human land-use activities (May et al. 2006; Krebs et al. 2007; Fisher et al. 2013b); and conversely, coyote positively respond to human altered landscapes (Šálek et al. 2014; Toews et al. 2017, 2018; Hody and Kays 2018). The significantly different response to landscape alteration will depend on species' relative niche breadth and hence flexibility (Crooks 2002; Rauset et al. 2012). Generalist species, such a coyote, better adapted to habitat change can expand their distribution patterns and increase in relative density. In contrast, specialist species, such as wolverine, are less likely to adapt and in turn lose range and population size, relegated to the more undisturbed areas. We might therefore infer that though the degree of dissimilarity between wolverine and coyote will reflect species-specific adaptations, but may also be a product of additive indirect effects of changing competition surfaces as a product of anthropogenic change. The plausibility of this mechanism warrants more investigation.

Furthermore, human-dominated landscapes are known to positively influence coyote densities by indirectly mediating interference competition from larger top predators such as wolves—being the apex predator—that are reduced or eliminated (Arjo and Pletscher 1999; Hebblewhite et al. 2005; Berger and Gese 2007). In relatively undisturbed areas where wolf and coyote home ranges overlap, large scale spatial and temporal segregation of these species allows for coexistence (Newsome and Ripple 2014). The significant increase of coyote occupancy along the east slopes of the Canadian Rocky Mountains suggests this region is on the advancing edge of a continental range shift at the community-level. Generalist carnivores, such as coyote, may act as a "distant early warning" of contemporary and future community shifts that pose threats to biodiversity and ecological stability. Contemporary study underscores the importance of evaluating whole carnivore community response to expanding human footprint globally (Burton et al. 2011).

Spatial community composition may be a valuable metric to evaluate ecological states and estimate the severity of cumulative impacts at a landscape scale. Attention to the severity of lag effects should therefore be considered paramount in preventing local extinction of the more sensitive species and mitigating the true and inordinate cost on local population diversity. As the cumulative impact is realized over space and time, we should expect to find widespread changes to carnivore community composition. While protected areas seek to conserve a full complement of native carnivores, examination of community composition may paint a different picture of realized effects. Additive to cumulative sources of habitat disturbance, indirect effects are likely to amplify interspecific interactions, shifting competition surfaces and further reducing suitable habitat for some carnivores. Thus, interspecific interactions are key to understanding carnivore species' spatial responses to landscape change: the varying outcomes of intra-guild competition coupled with niche-dependent species responses to changing resources, foiling the ecological generality ecologists seek.

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