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A specialized forest carnivore navigates landscape-level disturbance: Canada lynx in spruce-beetle impacted forests

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ABSTRACT

Canada lynx (*Lynx canadensis*) occupy cold wet forests (boreal and subalpine forest) that were structured by natural disturbance processes for millennia. In the Southern Rocky Mountains, at the species' southern range periphery, Canada lynx habitat has been recently impacted by large-scale disturbance from spruce beetles (*Dendroctonus rufipennis*). This disturbance poses a challenge for forest managers who must administer this novel landscape in ways that also facilitate timber salvage. To aid managers with this problem, we instrumented Canada lynx with GPS collars to document their selection of beetle impacted forests at spatial scales that spanned from landscapes to movement paths. We used a use-availability design based on remotely-sensed covariates to evaluate landscape- and path-level selection. We evaluated selection at the home-range scale in beetle-kill areas based on vegetation plots sampled in the field to quantify forest structure and composition. We found that across all scales of selection, Canada lynx selected forests with a higher proportion of beetle-kill trees that were generally larger in diameter than randomly available. Within home ranges, Canada lynx selected forests with greater live components of subalpine fir and live canopy of Engelmann spruce. During winter, Canada lynx exhibited functional responses, or disproportionate use relative to availability, for forest horizontal cover, diameter of beetle killed trees, live canopy of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*), and additive use (and consistent selection) for relative density of snowshoe hares and density of subcanopy subalpine fir 3–4.9 in. (7.6–12.4 cm) in diameter. We discuss our results in the context of balancing resource needs of Canada lynx with the desire to salvage timber in beetle-impacted forests.

1. Introduction

Forests provide vital services to ecosystems across the globe in terms of nutrient flow, water dynamics, habitat for species, and carbon sequestration (Iverson et al., 2018). Forests also offer spiritual and economic benefits to human communities in ways that are central to our general welfare (Iverson et al., 2018). Therefore, novel threats to the distribution and composition of forests often generate social and management actions with the aim of increasing resilience and persistence of forested ecosystems. Millar and Stephenson (2015) warn the novel threat from climate change is ushering in an era of "megadisturbance," where primarily fire and insect outbreaks threaten the structure and composition of forests worldwide. The threat of increased disturbance associated with a warming climate is especially concerning for cold wet forests (boreal and subalpine forest; Gauthier et al., 2015; Price et al., 2013; Seidl et al., 2016). Although large-scale disturbances traditionally drove successional trajectories within boreal forests (Agee, 2000; Eisenhart and Veblen, 2011; Price and Apps, 1995), it is generally acknowledged that warming and drying trends projected from continued climate change will increase the frequency and severity of disturbance at a scale that threatens the integrity of boreal ecosystems (Gauthier et al., 2015; Millar and Stephenson, 2015; Price et al., 2013; Sherriff et al., 2011). These changes could have far-reaching consequences, given that the boreal biome represents 25% of the Earth's closed canopy forests and plays a crucial role in the global carbon cycle (Boonstra et al., 2016).

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Outbreaks from spruce beetle (*Dendroctonus rufipennis*) and mountain pine beetle (*Dendroctonus ponderosae*) cause major disturbances across North America from boreal forests in Canada and Alaska (Berg et al., 2006; Campbell et al., 2019; Sherriff et al., 2011), and south through the subalpine forests of the Southern Rocky Mountains (Eisenhart and Veblen, 2011; Negrón and Cain, 2018). In Europe, spruce bark beetles (*Ips typographus*) are also responsible for unprecedented outbreaks in Norway spruce (*Picea abies;* Seidl et al., 2016). The underlying drivers of climate impacts on increased insect outbreaks are complex and include: altered patterns of temperature and precipitation/drought (Berner et al., 2017; Ramsfield et al., 2016; Sherriff et al., 2011), altered insect life cycles and demography (Bentz et al., 2010; Pureswaran et al., 2015; Ramsfield et al., 2016), shifts in host/insect phenology (Pureswaran et al., 2015), and changes in forest structure and composition (Campbell et al., 2019). A primary challenge facing current forest management is ameliorating the climate-induced impacts to forests for the benefit of society and the resilience of forested ecosystems (Millar and Stephenson, 2015). Compounding this ecological challenge are the social and economic pressures placed on forest managers to increase the salvage of beetle-killed trees to reduce the perceived risk of extensive wildfire and to provide local timber supplies (Fleming et al., 2002; Hart et al., 2015; James et al., 2017).

Evaluating different management alternatives that address disturbance at broad scales, such as large-scale tree salvage, is exceedingly difficult because various stakeholders have different justifications for selecting chosen management techniques (Iverson et al., 2018; Millar and Stephenson, 2015). This is especially true when management actions address large-scale disturbance on public, multiple-use lands where discussions also consider the habitat needs of sensitive species that are highly variable across taxa (Ivan et al., 2018; Saab et al., 2013). For example, salvage logging can reduce animal species richness, leading to substantial changes within ecological communities (Thorn et al., 2018), including reductions in populations of some small mammals (e.g., red-backed vole (*Myodes gapperi)*; Sullivan et al., 2010). However, other species such as ruffed (*Bonasa umbellus*) and spruce grouse (*Canachites canadensis*) may benefit from logging activities with responses being variable across species and tree harvest rates (Franklin et al., 2019). With respect to key predator and prey species in the boreal forest, Thomas et al. (2019) demonstrated that salvage logging can alter food webs over the short term (< 25 yr) by reducing snowshoe hare (*Lepus americanus*) abundance, which in turn directly influenced the presence of Canada lynx (*Lynx canadensis*) and coyotes (*Canis latrans*). Understanding how salvage logging, and related forest management, impacts both predator and prey is vital to maintain intact food webs in disturbed landscapes (Estes et al., 2011).

Canada lynx are an iconic predator of the boreal and subalpine forest ecosystems and an ideal species to investigate response to large-scale disturbances, such as insect outbreaks. In the contiguous U.S., Canada lynx is a federally-listed carnivore under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service, 2000). This requires federal agencies to understand how tree salvage or other disturbances may impact the species. In addition, Canada lynx are of interest to ecologists concerned with climate change, because they are specialized forest carnivores that are restricted to deep-snow environments found in boreal and subalpine forests (Agee, 2000; Mowat et al., 2000). At the southern range periphery, Canada lynx are highly selective in their use of forest structure and composition (Ivan and Shenk, 2016; Koehler et al., 2008; Simons-Legaard et al., 2013; Squires et al., 2010). Canada lynx in the Northern Rocky Mountains exhibit a positive demographic response to the connectivity of mature subalpine forests within home ranges (Holbrook et al., 2019a, 2019b; Kosterman et al., 2018) and they exhibit functional responses to forest-structure classes (Holbrook et al., 2017a) and to specific silvicultural practices (Holbrook et al., 2018). Similar to northern populations (Mowat et al., 2000), the ecology of Canada lynx at the southern range periphery is strongly driven by their dependence on snowshoe hares as primary prey (Ivan and Shenk, 2016; Squires and Ruggiero, 2007) that require forest with high horizontal cover (Hodges, 2000; Holbrook et al., 2017b). Thus, Canada lynx at the southern range periphery might be particularly sensitive to large-scale fire and insect disturbances that alter forest structure and composition of boreal and subalpine forests for potentially many decades.

In our study, we investigated how Canada lynx (used interchangeably as "lynx" hereafter) navigated a novel landscape created by a spruce-beetle outbreak at the southern tip of the species' range. We used GPS telemetry to relate the movement patterns of lynx to measures of environmental heterogeneity in spruce beetle-impacted forests. Our overarching goal was to provide forest managers with conservation insights and tools that distinguished forest stands essential to the conservation of Canada lynx from those stands that were less important and therefore available for timber salvage with little impact to this federally-listed species. This work also required novel advancements in mapping of tree canopy and subcanopy characteristics in beetle-impacted stands using remote sensing (i.e., Savage et al., 2017).

To achieve our goal, we implemented a 3-step analytical process. We first evaluated patterns of *habitat use* and resource *selection* (Boyce et al., 2002; Johnson et al., 2004; Lele et al., 2013) of Canada lynx in beetle-impacted landscapes at multiple spatial scales. At the broadest scale, we determined the environmental features that lynx selected or avoided when establishing a home range (second-order selection; Johnson 1980). We then measured stand metrics useful to foresters and silviculturists at locations used by lynx and compared that to random locations within lynx home ranges (third-order selection). At the finest scale, we evaluated what resources lynx were selecting on a sequential basis along their movement path (fourth-order selection). This is commonly referred to as step-selection (Fortin et al., 2005). In our second analytical step, we evaluated how lynx use of differing resources (e.g., forest subcanopy) changed as the resource became more or less available. This is termed a functional response in habitat use (Holbrook et al., 2019a, 2019b; Mysterud and Ims, 1998), which can provide additional insight about the behavioral importance of a particular habitat attribute. Lastly, we developed predictive maps of habitat suitability (e.g., DeCesare et al., 2012; Squires et al., 2013) for Canada lynx across the beetle-impacted landscape to help spatially inform forest management actions. These maps are a valuable tool for managers to efficiently identify areas of importance for Canada lynx conservation relative to those areas that are less important, which could be prioritized for focused timber salvage. Collectively, our research advances the applied ecological understanding of how a highly specialized forest carnivore responded to broad-scale changes in montane forests, while also informing forest management actions.

Based on literature and our long-term research experience with Canada lynx, we developed multiple predictions. Western populations of Canada lynx in the contiguous U.S. are generally restricted to mixed-conifer forests dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) with live overstory canopy (Aubry et al., 2000; Ivan and Shenk, 2016; Squires et al., 2010). Lynx associate with a mosaic of forest age and structure classes to meet their foraging needs and other life-history requirements (Holbrook et al., 2017a; Squires et al., 2010). This mosaic includes a structure class of mature forest at the species' southern periphery (Holbrook et al., 2017a, 2017b; Ivan and Shenk, 2016; Simons-Legaard et al., 2013; Squires et al., 2010). Therefore, we predicted that Canada lynx would select home ranges with forest structures that were most consistent with mature, spruce-fir forests (live canopy) within beetle-impacted landscapes. Thus, we expected that Canada lynx, when confronted with a highly altered landscape from spruce beetle impacts, would select for patches of live canopy cover with dense sub-canopies of Engelmann spruce and subalpine fir, and for mature green forests to the extent possible (Holbrook et al., 2017a; Ivan and Shenk, 2016; Squires et al., 2010). Second, we predicted that Canada lynx within home ranges and along movement paths would select forest stands with higher understory (high horizontal cover) compared to random locations. We based this prediction on the

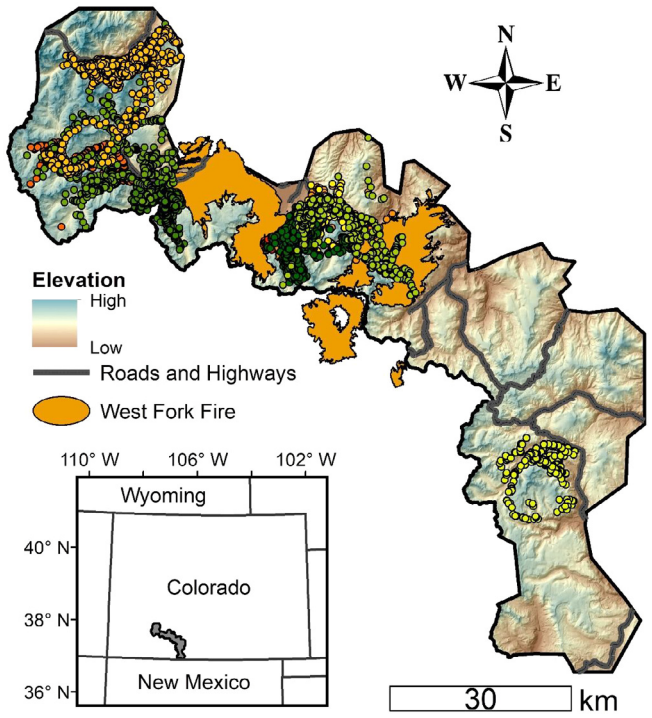


Fig. 1. Canada lynx (*Lynx canadensis*) study area on the Rio Grande National Forest in southwestern Colorado, USA, with lynx GPS locations displayed (color of points changes with individual lynx).

numerical response of snowshoe hares to forest stands with high horizontal cover (Griffin and Scott Mills, 2009; Hodges, 2000; Holbrook et al., 2017b). We expected spruce beetle outbreaks could decrease overall horizontal cover in spruce-fir stands due to the high mortality of Engelmann spruce; this assumes that large, mature Engelmann spruce trees contribute substantially to horizontal cover within our landscape. However, within this altered landscape, we assumed that lynx and hares would be associated with the highest horizontal cover available within beetle-impacted stands. Finally, we predicted that Canada lynx would become increasingly selective (i.e., a functional response) for forest structures associated with horizontal cover (i.e., high subcanopy cover) in areas where horizontal cover was sparsely distributed.

2. Methods

2.1. Study area

Our study area (3,466 km^2) was located in the San Juan Mountains of southern Colorado, USA (location centroid 37.554 Lat, −106.868 Lon; Fig. 1) and was administered as public land by the U.S. Forest Service, Rio Grande National Forest. Topography of the San Juan Mountains was typical of the Southern Rocky Mountains with steep mountain valleys punctuated with high peaks across an elevation range of approximately 2000–4300 m asl. The high topographic relief provided a mosaic of montane conifer forests interspersed with meadows and avalanche paths extending up to alpine tundra. The subalpine boreal forests that supported Canada lynx (elevation 2500–3500 m asl) were dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Other conifers present included Douglas-fir (*Pseudotsuga menziesii*), bristlecone pine (*Pinus aristata*), limber pine (*Pinus flexilis*), and blue spruce (*Picea pungens*). Aspen (*Populus tremuloides*) was common on disturbed slopes and was inter-mixed with conifers in mid-seral stands. Lodgepole pine (*Pinus contorta*) was absent from the study area except in small plantations. Willow (Salix spp.) occurred in high elevation meadows and riparian bottomlands. Winters extended from November through May (low elevations) and some snow cover persisted into June. Annual snowfall was approximately 380 cm to 1000 cm and low winter temperatures averaged approximately −13 °C with high summer temperatures approximately 23 °C (National Oceanic and Atmospheric Administration, 2017).

Prior to 2002, the subalpine boreal forests on our study area were dominated by stands composed of mostly mature trees approximately 200–350 years in age; some trees on the Rio Grande National Forest exceeded 600 years (Ryerson et al., 2003; Whipple and Dix, 1979). In 2004, spruce beetles caused mortality to primarily Engelmann spruce trees. The beetle outbreak then intensified such that 10% of the study area was impacted by 2007, 20% by 2010, 30% by 2012, 40% by 2014, after which insect activity began to plateau at nearly 50% impact by 2016 (U.S. Forest Service Forest Health Protection, 2017). In addition, the study area was impacted by an extensive (200 km^2) fire in 2013 (the West Fork Complex; Fig. 1). We did not investigate lynx use of this fire as a part of our research.

2.2. Canada lynx capture and handling

Approximately 85% of the 218 Canada lynx reintroduced to Colorado from 1999 to 2007 were released on the Rio Grande National Forest, and this region remains some of the most important occupied lynx habitat in the state (Devineau et al., 2010). Given that Canada lynx on our study area were reintroduced over 20 years ago, the adult population represented the second-generation of those founders, and these adults have demonstrated successful reproduction (Devineau et al., 2010). From 2015 to 2017, we captured 10 adult (> 3 years old) Canada lynx (6 males and 4 females) in box traps (Kolbe et al., 2003) that were set on travel paths identified by snow tracks during winter months (December to March); traps were checked every 24 h. Our sample of Canada lynx included most individuals present on the study area, based on our field observations. We instrumented Canada lynx with store-on-board GPS collars (210–230 g; (Telemetry Solutions, Concord, California, USA) equipped with remote download capability from aircraft and VHF beacon transmitters. Collars were also equipped with a drop-off mechanism that automatically activated following summer sampling, usually by early August. All capture and handling procedures were conducted under the guidelines of Animal Care and Use Permit # CPW ACUC File #01-2015.

2.3. Data collection

GPS locations provided the foundation for our multi-scale assessment of habitat use and resource selection by Canada lynx within beetle-impacted forests during both winter (January – April) and summer (May – August). Given that Canada lynx exhibit seasonal differences in resource use (Squires et al., 2010), we programmed collars for a location attempt every 68 min during the winter (January 1 – April 15) and summer (June 1 – August 15) sampling seasons, with a lower fix rate (360 min) otherwise. All Canada lynx incorporated in the study exhibited movements that were consistent with resident individuals with established home ranges. We recorded 802 – 1,715 locations per individual during winter (11,628 total winter GPS locations, 10 lynx) and 895 – 1,272 locations per individual during summer (7,721 total summer GPS locations, 7 lynx). Because of collar failures shortly after deployment, our summer sample size was smaller than our winter sample. We did not correct for potential habitat-induced bias in data acquisition, because our GPS mean fix-rate was high ($\bar{x}$=88%) across individuals (Hebblewhite et al., 2007).

2.4. Multi-scale resource selection

2.4.1. Selection across landscapes - Second order

At the landscape scale (i.e. second-order selection), we evaluated resource selection separately during winter and summer by comparing

lynx GPS locations to random locations distributed throughout our study area. The density of available points was 1 location/500 m^2 and each random location could be no closer than 100 m from another random location. We generated a unique sample of 7,000 available points for each lynx which resulted in a use to availability ratio ranging from 1:4 to 1:9 across individual lynx during both seasons. This ensured appropriate coverage of availability for all lynx while sampling such that the ratio of use:availability for each lynx far exceeded the ratio necessary to generate stable coefficients for a patchy, heterogeneous landscape (Northrup et al., 2013). We then developed seasonal resource selection functions (RSFs; Boyce et al., 2002; Johnson et al., 2006; Manly et al., 2002) at the landscape scale using mixed-effects logistic regression (logit link), treating individual lynx as the random intercept. This structure allowed us to account for (1) unbalanced sampling among individual lynx, and (2) repeated measures (GPS locations) within lynx (Gillies et al., 2006). By implementing this structure, we assumed lynx might have different selection intensities, but that the general preference or avoidance with respect to environmental resources was similar. This structure also allowed us to efficiently develop spatial predictions of relative probability of lynx use across the landscape. Our RSF structure was as follows:

$$w(x) = \exp(\beta_1 x_{1j} + \beta_2 x_{2j} + \cdots + \beta_i x_{ij} + \gamma_{0j}), \quad (1)$$

where β_i is the population-level (i.e., marginal) RSF coefficient for covariate i, x_{ij} is the value of covariate i for individual j, γ_{0j} is the random intercept associated with the jth animal, and $w(x)$ is the predicted relative probability of use (Boyce et al., 2002).

We based our evaluation of landscape-scale selection on remotely-sensed covariates that described biotic, abiotic, and anthropogenic gradients across our study area (Table 1). For biotic covariates at used and available locations, we calculated the mean value (± 95 CIs) of dead forest canopy (at the 100 × 100 m neighborhood), as well as live canopy cover and subcanopy density for the following tree species: subalpine fir, Engelmann spruce, quaking aspen, and Douglas-fir. Our covariates of tree species composition were developed for our study area in a previous study by Savage et al. (2017) using Landsat imagery and topographic gradients.

We characterized our abiotic gradients with four covariates (Table 1): long-term precipitation (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, retrieved January 2017), topographic roughness (Jenness, 2004), topographic position index (Jenness, 2006), and a heat load index (McCune and Keon, 2002). We expected Canada lynx in the Southern Rocky Mountains to select areas of relatively mild topography, cool-moist conditions, and areas characterized as basins versus ridges (e.g., Holbrook et al., 2017a; Squires et al., 2008, 2013). Previous work in the Northern Rocky Mountains indicated Canada lynx prefer areas of intermediate elevations and thus intermediate snow accumulations (Holbrook et al., 2017b; Ivan et al., 2014; Squires et al., 2013); that is, selecting areas in between alpine habitats and valley bottoms. Therefore, we expected to observe a similar pattern with respect to Canada lynx selection of long-term precipitation.

Finally, we incorporated two covariates associated with the distribution and density of roads. We evaluated the selection response of lynx to the density of paved roads and highways as well as to the density of non-paved roads maintained by the U.S. Forest Service (USFS; Table 1). We did not expect roads to influence selection behavior of Canada lynx *per se* (Baigas et al., 2017). However, based on the distribution of roads in our study area we expected lynx to select greater USFS road density and avoid paved roads and highways, since USFS roads were largely constructed to facilitate timber harvest whereas paved roads and highways were primary transportation corridors that generally followed valley bottoms.

We implemented a multi-step process to execute our RSF modeling. For all landscape covariates with a base resolution of 30 × 30 m (Table 1), we summarized variables to 100 m, 250 m, and 500 m neighborhoods and evaluated which scale and function (linear or quadratic) was most supported by the data using Akaike's Information Criteria, corrected for small sample sizes (AIC_c; Anderson and Burnham, 2002; Burnham and Anderson, 2002). Similar to Holbrook et al. (2017a), we initially created a suite of univariate mixed-effects models for each covariate and evaluated how they compared to an intercept-only model (null model). We removed all covariates from consideration that were not ≥ 2 ΔAIC_c values better than the null model. This initial univariate screen ensured that all covariates in models were biologically meaningful to Canada lynx resource selection. We then explored correlations among variables and prevented those that exhibited an $|r| > 0.60$ from entering the same model. Because we were interested in both understanding habitat selection by Canada lynx, as well as developing predictive habitat suitability maps, we searched for the best abiotic model (precipitation, topographic, and anthropogenic variables in Table 1) using an all-subsets approach. With the best abiotic model identified, we then evaluated our initial predictions concerning how Canada lynx may respond to novel forest conditions found in spruce beetle-impacted forests by adding combinations of biotic variables from our suite of covariates. For all variable and model selection choices, we assessed support using AIC_c and standardized regression coefficients to determine relative effect sizes. We performed all analyses using standard tools in ArcGIS (ESRI 2019. ArcGIS Desktop: Release 10.5.1. Redlands, CA: Environmental Systems Research Institute) as well as the

Table 1
Resource variables used in analyses of landscape-scale habitat selection for Canada lynx (*Lynx canadensis*) in spruce beetle (*Dendroctonus rufipennis)*-impacted forests of southwestern Colorado, USA. Covariate codes POTR, PIEN, ABLA, PSME indicate quaking aspen (*Populus tremuloides*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and Douglas-fir (*Pseudotsuga menziesii*), respectively.

Theme	Variable	Units	Base Resolution	Reference
Canopy	Total mortality	%	30 × 30 m	Savage et al. (2017)
	POTR canopy cover	%	30 × 30 m	Savage et al. (2017)
	PIEN canopy cover	%	30 × 30 m	Savage et al. (2017)
	ABLA canopy cover	%	30 × 30 m	Savage et al. (2017)
	PIEN-ABLA canopy cover	%	30 × 30 m	Savage et al. (2017)
Live sub-canopy	PSME tree count	Count	30 × 30 m	Savage et al. (2017)
	POTR tree count	Count	30 × 30 m	Savage et al. (2017)
	PIEN tree count	Count	30 × 30 m	Savage et al. (2017)
	ABLA tree count	Count	30 × 30 m	Savage et al. (2017)
	PIEN-ABLA tree count	Count	30 × 30 m	Savage et al. (2017)
Precipitation	Mean annual precipitation over 1981–2010	mm	800 × 800 m	PRISM Climate Group, Oregon State University 2017
Topographic	Roughness	Index	30 × 30 m	Jenness (2004)
	Heat load index	Index	30 × 30 m	McCune and Keon (2002)
	Topographic position index	Index	30 × 30 m	Guisan et al. (1999)
Anthropogenic	Density of major roads and highways	m/ha	1 × 1 km	Colorado Department of Transportation 2010
	Density of USFS roads	m/ha	1 × 1 km	Rio Grande National Forest 2017

statistical program R (R Core Team, 2019).

2.4.2. Selection within home-ranges – Third order

To understand how Canada lynx responded to stand-level characteristics in beetle-impacted forests (third-order selection within home ranges; Johnson, 1980), we measured forest attributes at winter and summer GPS locations of lynx as compared to random from 2015 to 2017. We calculated 95% fixed kernel home ranges for both winter and summer to provide a biologically meaningful definition of availability for each lynx (Calenge, 2006). We balanced the sample for used and available locations equally (approximately 1:1). Thus, we sampled 457 used and available plots in the field during the winter (41–52 plots per lynx) for 10 individuals (4 females, 6 males) and 278 used and available plots during summer (43–50 plots per lynx) across 6 animals (4 females, 2 males). Vegetation sampling was conducted primarily the season following lynx-use.

We quantified forest and other environmental attributes on 400 m^2 (11.2 m radius) circular plots. These included measures of tree and other vegetation metrics, horizontal cover, woody debris, and relative snowshoe hare density (see plot configuration in Appendix A). For trees (≥3 in or 7.6 cm DBH diameter), we recorded: species, diameter at breast height (DBH), and condition (live, dead via beetle kill, snags). We estimated canopy cover on a 25-point, 20 × 20 m grid established at plot center. At each grid point, we determined canopy presence or absence using a vertical projection tube (i.e., moosehorn; Fiala et al., 2006). We then processed tree-plot data using the USFS, Forest Vegetation Simulator (FVS) software version that accounted for conditions in the Central Rocky Mountains and the San Juan National Forest (Dixon, 2002). For live trees (53% of all trees), we calculated tree density overall and per acre (0.405 ha) by species (TPA), quadratic mean diameter (QMD), basal area (BA), canopy cover, and stand density index (SDI). The tree species that accounted for most (98.5%) live trees on plots included: 35% subalpine fir (ABLA), 24% Engelmann spruce (PIEN), 34.5% quaking aspen (POTR), and 5% blue spruce (PIPU). In addition, we calculated the TPA for each species by four different size classes: 7.6–12.5 cm (3–4.9 in), 12.7–22.6 cm (5–8.9 in), 22.9–40.4 cm (9–15.9 in); and ≥ 40.4 cm (≥16 in.). For dead, beetle-killed trees (35% of all trees), we calculated the same metrics, except SDI. The composition of dead trees was: ABLA (11.5%), PIEN (73.5%), and POTR (12%). The dead trees of PIEN (85%) and ABLA (13%) together accounted for 98% of the beetle-impacted trees. Finally, for snags (12% of all trees), we calculated overall TPA, QMD, and BA. We distinguished snags from beetle-killed trees based on their lack of horizontal branching and their general appearance of being older than the beetle outbreak (therefore, the source of mortality was unknown, but could have been from beetles prior to the epidemic outbreak).

We also sampled the species composition and density of subcanopy trees (> 1 m height) present on plots using a 1-m belt-transect centered on a 22.4 m line that defined the north–south axis of the plot (Appendix A). We recorded the species and height of all subcanopy trees present in the belt-transect. Nearly all subcanopy trees were < 6 m (19 ft) in height; 90% were < 4.5 m (15 ft) and 85% were < 3 m (10 ft). From the plot center, we measured horizontal cover, which is associated with density of small trees in the understory (Holbrook et al., 2017b; Squires et al., 2010). We estimated horizontal cover at 10 m in each of the four cardinal directions using a 2 m tall × 0.50 m wide coverboard divided into four 0.50 × 0.50 m blocks (16 readings averaged/plot). Finally, we estimated the relative abundance of snowshoe hares by counting fecal pellets on uncleared, 1-m circular plots (Murray et al., 2002) distributed every 5.6 m along the 22.4 m line (we recorded 5 pellet counts per vegetation plot). Many studies have documented the close relationship between fecal pellet counts and snowshoe hare densities (Berg and Gese, 2010; Krebs et al., 1987; Mills et al., 2005; Murray et al., 2005).

Similar to our landscape-scale modeling, we implemented a multi-step process to complete our RSF modeling at the home range scale. To reduce the number of potential variables (i.e., 120 variables) to include those most biologically meaningful to lynx, we initially created a suite of univariate mixed-effects models (logistic regression with lynx as random effect) similar to the procedures we used at the landscape scale for each covariate. We retained covariates that performed better than the intercept-only model (null model) based on ΔAIC_c and we removed covariates with high correlations (i.e., $|r| > 0.60$); we selected the covariate with the lower AIC_c value when two variables were correlated. We further evaluated this reduced set of candidate covariates with the Least Absolute Shrinkage and Operator (LASSO; Groll and Gerhard, 2014) to identify the most predictive candidate variables (i.e., those that did not shrink to approximately 0). We assessed lambda values (the log-likelihood penalty term) between 0 and 500 within the LASSO and selected the optimal lambda using AIC_c. Finally, we searched all-subsets of models using the variables identified in the LASSO and selected the top model(s) using AIC_c. We used generalized linear mixed-models (logistic regression with a random intercept for lynx) for all model-based analyses (i.e., univariate models, LASSO, and model-selection) and, similar to our landscape-scale analyses, we estimated standardized regression coefficients for our top selected models. We performed all analyses using the software program R (R Core Team, 2019).

2.4.3. Selection along movement paths - Fourth order

We employed step selection functions (Fortin et al., 2005; Thurfjell et al., 2014) to investigate how Canada lynx selected forest attributes, conditional on local availability, as they moved through the beetle-impacted landscape. Step-selection functions compare used locations (GPS locations at time t) along a movement path to random locations generated from the same starting point (the GPS location at time $t - 1$). These random locations are developed based on the movement characteristics of the animal (e.g., the distribution of turn angles and step lengths between successive GPS locations) and thus characterize a limited domain of availability along a movement path. In our case, SSFs helped us evaluate what habitat resources lynx consistently moved toward versus those resources they consistently avoided along their movement path.

We evaluated a series of focused questions concerning lynx movement during winter (n = 10 lynx; 4 females, 6 males) and summer (n = 7 lynx; 4 females, 3 males). We only evaluated how lynx responded to forest-based covariates that were uncorrelated, well distributed across lynx movement paths (i.e., available for selection), and were relevant to forest management and lynx ecology. Our covariates of interest included percent canopy cover and subcanopy tree count of subalpine fir and Engelmann spruce, as well as the percent total mortality in the canopy (Savage et al. 2017; Table 1). Covariates were averaged to a 100 × 100 m resolution, which ensured they were relevant to lynx movement patterns (Thurfjell et al., 2014). For instance, median step length across lynx and seasons was ≈50 m, which corresponded to half the window length/width used to summarize our covariates. We sampled our winter (n = 8545 lynx GPS locations) and summer (n = 5160 lynx GPS locations) used data to ensure (1) time intervals were consistent with our target interval of 68-min between GPS locations, and (2) each track was composed of ≥2 successive GPS locations (i.e., need to know start and end points to include a step in the analysis). For each used step, we generated a random sample of 15 available steps from a gamma distribution to each individual's step lengths and a von Mises distribution to each individual's turn angles (Avgar et al., 2016). We extracted covariate values at the endpoints of used and random steps and implemented conditional logistic regression to estimate selection coefficients in a matched case-control design, where strata were assigned to each set of used and random steps along the movement path. We also incorporated step length as a variable in our models to reduce potential bias in coefficient estimates associated with dependence between used and available steps (Forester et al., 2009). We fit a single global model including all 5 covariates to each individual lynx during winter and summer and recorded the selection

coefficient along with the 95% CI. We conducted our analyses using the 'amt' package (Signer et al., 2019) in the software program R (R Core Team, 2019).

2.5. Predictive performance of landscape RSF models and habitat suitability mapping

We produced habitat suitability maps (predictions of relative probability of animal use) to inform land management and conservation planning (Hebblewhite et al., 2014; Johnson et al., 2006; Morris et al., 2016). We performed 2 assessments to validate predictions characterizing relative probability of use for Canada lynx at the landscape-level. First, we implemented a leave-one-out cross-validation, which is a technique to determine the robustness of a model's predictions (Matthiopoulos et al., 2011). We sequentially withheld each individual lynx, re-ran our top RSF model on the remaining lynx, and used the withheld lynx to test the model's ability to predict resource use. Second, we used the population-level β coefficients and Eq. (1) to develop putative landscape-level suitability maps for lynx at a 30 × 30 m resolution, which we categorized into 10 equal-area bins from low to high predicted lynx use. Prior to all analyses, we withheld 10% of the GPS locations for each lynx for model validation. We overlaid our withheld lynx data (n = 1109 winter GPS locations, n = 780 summer GPS locations) on our putative habitat maps derived from our top RSF models. For both assessments (winter, summer), we evaluated how the bin frequency of withheld lynx use correlated with predicted lynx use using Spearman rank correlation coefficients (Boyce et al., 2002).

Forest managers and conservationists generally can use at least two versions of habitat suitability maps to inform their decision-making processes: a continuous map and a binary map. To develop a continuous habitat suitability map for Canada lynx, we simply used the β coefficients derived from our landscape-scale RSF model and Eq. (1) to predict lynx-use of spruce beetle-impacted forests across our study area (similar to DeCesare et al., 2012; Hebblewhite et al., 2014; Holbrook et al., 2017a). Continuous maps are the most commonly produced habitat suitability maps; however, binary maps are often helpful for land management decision making and planning where thresholds are required. For example, one of our goals was to identify, at a landscape scale, those areas in beetle-impacted forests that are central to the conservation of Canada lynx versus areas where salvage logging would have little impact. A binary map is useful to address this question within a management context. To develop our binary map, we used an approach similar to Holbrook et al. (2017a) to identify a cut-point through the continuous map that characterized low versus high relative probability of lynx use. We examined how the cumulative percentage of withheld lynx GPS locations were distributed across our 10 equal-area bins of lynx use, from *high* to *low*. We assessed how many bins (again, from high to low probability of lynx use) were required to capture 95% of the withheld Canada lynx locations, which we defined as 'selected' habitat, whereas the bins capturing the remaining 5% of lynx locations we defined as 'less selected.' The 95% threshold here is analogous to a 95% home range in that both are capturing the top 95% of an animal's use. The threshold used to create a binary map can be modified, and is ultimately a management-based decision. We used standard tools in ArcGIS (ESRI 2019. ArcGIS Desktop: Release 10.5.1. Redlands, CA: Environmental Systems Research Institute) and the software program R (R Core Team, 2019) to produce our habitat suitability maps.

2.6. Functional responses in habitat use across home ranges

To complement our third-order RSF analyses, we evaluated if Canada lynx exhibited functional responses to the novel environmental features in home ranges following the spruce-beetle outbreak (Holbrook et al., 2019a, 2019b; Moreau et al., 2012; Mysterud and Ims, 1998; van Beest et al., 2015). This assessment provided insight concerning the consistency of how Canada lynx may alter their use of forest resources. We evaluated the question of how resource use by lynx changed as resource availability shifted across lynx home ranges. We only evaluated functional responses in habitat use for those covariates that received the strongest selection or avoidance (i.e., were included in our top third-order RSF model) during both winter and summer. We characterized resource use and availability by calculating the mean (and SE) of each covariate at used and available locations for each individual (Holbrook et al., 2017a, 2019a, 2019b). We then fit linear models through the data points from all individuals to test for a functional response in habitat use:

$$\bar{m}^U(x_1) = \theta_0 + \theta_1(\bar{m}^A(x_1)) \quad (2)$$

where, $\bar{m}^U(x_1)$ = a vector (across individuals) of mean values for resource x_1 at used units, $\bar{m}^A(x_1)$ = a vector (across individuals) of mean values for resource x_1 at available units, θ_0 = y-intercept, and θ_1 = slope of the functional response term. Statistical deviations from proportional habitat use ($\theta_1 = 1$) could indicate a preference in habitat use ($\theta_1 > 1$) for an environmental attribute, whereas a decreasing term ($\theta_1 < 1$) suggested resource avoidance. We performed all analyses of functional responses in the statistical program R (R Core Team, 2019).

3. Results

3.1. Multi-scale resource selection – From landscapes to movement paths

Canada lynx exhibited differing patterns of selection for biotic and abiotic resources at the landscape-scale based on remotely-sensed covariates. Our top RSF models for winter and summer were nearly identical in that they contained similar sets of covariates and all effects were statistically significant (Table 2). There was no model uncertainty; the next closest models were 90 and 14 ΔAIC_c values away from our top models in winter and summer, respectively (Appendix B). All abiotic covariates were included in the top model for winter and summer, however, there were some differences in terms of lynx selection and avoidance between the seasons. For instance, lynx avoided topographically rough areas and selected locations with higher heat loads during the winter months, whereas in the summer, lynx behavior was the opposite (Table 2). For the remaining abiotic covariates, lynx exhibited similar responses across seasons. Lynx selected basins, areas with intermediate amounts of long-term precipitation (i.e., avoided low and high precipitation areas), and higher densities of USFS roads; they avoided ridgelines and major roads and highways (Table 2). We believed the relationship for lynx-use of these linear features was a function of how forest roads and highways were associated with adjacent forest characteristics rather than an attraction or avoidance of human activity *per se*.

Of particular interest to our research was the response of Canada lynx at the landscape-scale to biotic components found in beetle-impacted forests given the desire for tree salvage and active forest management. We found that Canada lynx exhibited a strong preference for landscapes with a high proportion of beetle-killed trees during both winter and summer seasons; this relationship was consistent in univariate assessments (Fig. 2) and multivariate models (Table 2). During winter, Canada lynx used areas with quaking aspen in the canopy and more live Engelmann spruce and subalpine fir in the subcanopy. During summer, lynx tended to avoid areas with live Engelmann spruce in the canopy, but preferred areas with higher levels of spruce in the subcanopy. Canada lynx consistently avoided areas with higher levels of Douglas-fir in the subcanopy regardless of season.

In contrast to the landscape-scale, top models at the home-range scale (i.e., third-order of selection and based on forest metrics measured in the field) contained mostly different sets of forest covariates between winter and summer (Table 3). Canada lynx consistently (and statistically; $p < 0.10$) selected for areas with higher horizontal cover and relative snowshoe hare density during both winter and summer seasons

Table 2
Seasonal resource selection results for Canada lynx (*Lynx canadensis*) in spruce beetle (*Dendroctonus rufipennis)*-impacted forests at the landscape-scale (second-order selection; Johnson 1980) in southwestern Colorado, USA. Standardized marginal coefficients, standard errors (SE), and *p*-values from our most parsimonious mixed-effects resource selection function (RSF). Covariate codes POTR, PIEN, ABLA, PSME indicate quaking aspen (*Populus tremuloides*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and Douglas-fir (*Pseudotsuga menziesii*), respectively. All variables significant at $P < 0.001$.

Season	Theme	Covariate	β	SE
Winter (n = 10 lynx)	Abiotic	Roughness	−0.183	0.012
		Heat load index	0.195	0.013
		Topographic position index	−0.078	0.012
		Mean annual precipitation over 1981–2010	−1.682	0.031
		Mean annual precipitation over 1981–2010^2	−0.499	0.020
		Density of major roads and highways	−0.449	0.022
		Density of USFS roads	0.457	0.012
	Forest	Dead canopy	0.672	0.015
		POTR canopy	0.129	0.013
		PIEN-ABLA subcanopy	0.247	0.014
		PSME subcanopy	−0.391	0.022
Summer (n = 7 lynx)	Abiotic	Roughness	0.735	0.016
		Heat load index	−0.209	0.014
		Topographic position index	−0.076	0.014
		Mean annual precipitation over 1981–2010	−1.305	0.035
		Mean annual precipitation over 1981–2010^2	−0.469	0.024
		Density of major roads and highways	−0.413	0.032
		Density of USFS roads	0.490	0.016
	Forest	Dead canopy	0.815	0.020
		PIEN canopy	−0.613	0.030
		POTR canopy	0.074	0.018
		PIEN subcanopy	0.343	0.026
		PSME subcanopy	−0.911	0.052

Table 3
Seasonal resource selection results for Canada lynx (*Lynx canadensis*) in spruce beetle (*Dendroctonus rufipennis)*-impacted forests at the home-range scale (third-order selection; Johnson 1980) in southwestern Colorado, USA. Standardized marginal coefficients, standard errors (SE), and *p*-values from our most parsimonious mixed-effects resource selection function (RSF). Covariate codes POTR, PIEN, ABLA, PSME indicate quaking aspen (*Populus tremuloides*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and Douglas-fir (*Pseudotsuga menziesii*), respectively, while QMD, TPA, DBH, and BA indicate quadratic mean diameter (1 in. = 2.54 cm), trees per acre (1 acre = 0.405 ha), diameter at 4.5 feet (1 foot = 30.48 cm), and basal area.

Season	Covariate	β	SE	*p*
Winter (n = 10 lynx)	Horizontal cover	0.239	0.124	0.054
	Snowshoe hare pellets	0.245	0.132	0.063
	Canopy cover of live PIEN	0.353	0.118	0.003
	QMD of live ABLA	0.267	0.121	0.027
	QMD of live POTR	0.321	0.113	0.004
	QMD of dead trees	0.366	0.152	0.016
	TPA of live ABLA 3–4.9 in. in DBH	0.328	0.145	0.023
	TPA of dead PIEN 5–8.9 in. in DBH	0.328	0.143	0.022
	BA of dead trees	−0.319	0.161	0.047
Summer (n = 6 lynx)	Horizontal cover	0.427	0.139	0.002
	Snowshoe hare pellets	0.231	0.139	0.078
	QMD of dead PIEN	0.492	0.142	0.001
	QMD of dead ABLA	0.263	0.135	0.051

(Table 3). During the winter months, lynx exhibited strong selection for areas with higher canopy cover of live Engelmann spruce trees, larger live subalpine fir and quaking aspen trees, and higher densities of live subalpine fir trees 7.6–12.4 cm (3–4.9 in. in diameter). In addition, during winter lynx avoided areas with more basal area of dead trees, but lynx strongly selected areas with larger dead trees and areas with higher densities of dead Engelmann spruce trees 12.7–22.6 cm (5–8.9 in.) in diameter (Table 3). During the summer months, the size of beetle-killed subalpine fir and Engelmann spruce trees were two additional covariates in our top model of lynx selecting high horizontal cover and snowshoe hare densities. Lynx exhibited selection for areas with larger dead subalpine fir trees and demonstrated strong selection

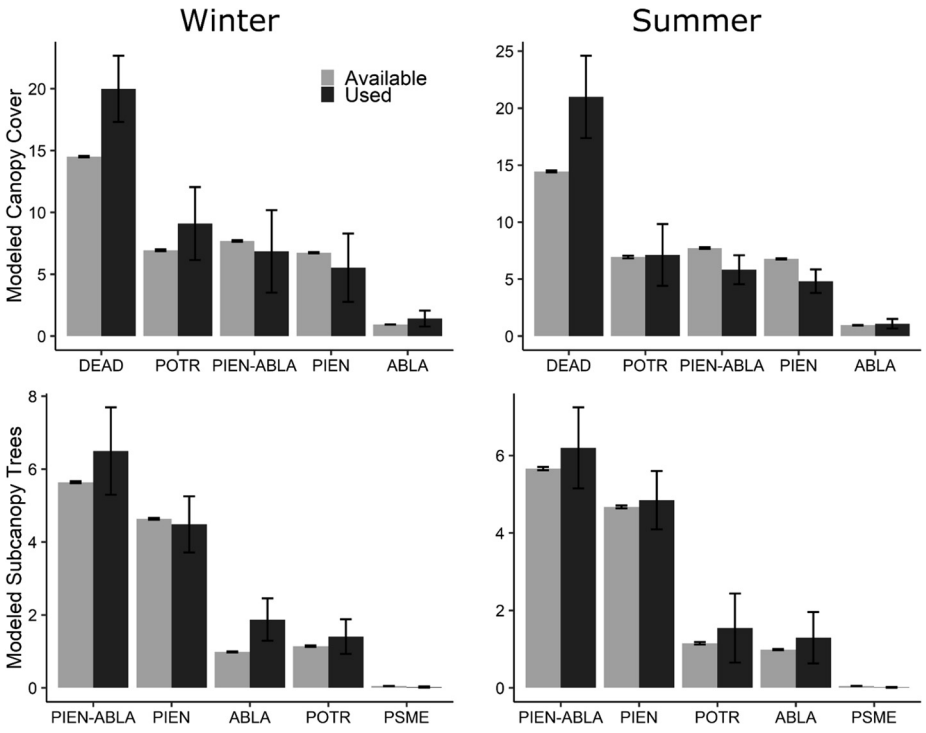


Fig. 2. Canada lynx (*Lynx canadensis*) habitat use (mean ± 95% CIs) of canopy cover by tree species, tree mortality from spruce-beetle (*Dendroctonus rufipennis)* outbreak, and subcanopy trees at the landscape scale in southwestern Colorado, USA. Means were calculated across lynx at used and available locations. Forest metrics were quantified from remotely sensed variables using methods developed by Savage et al. (2017). Covariate codes POTR, PIEN, ABLA, PSME, and DEAD indicate quaking aspen (*Populus tremuloides*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), Douglas-fir (*Pseudotsuga menziesii*), and percent total tree mortality in the canopy, respectively.

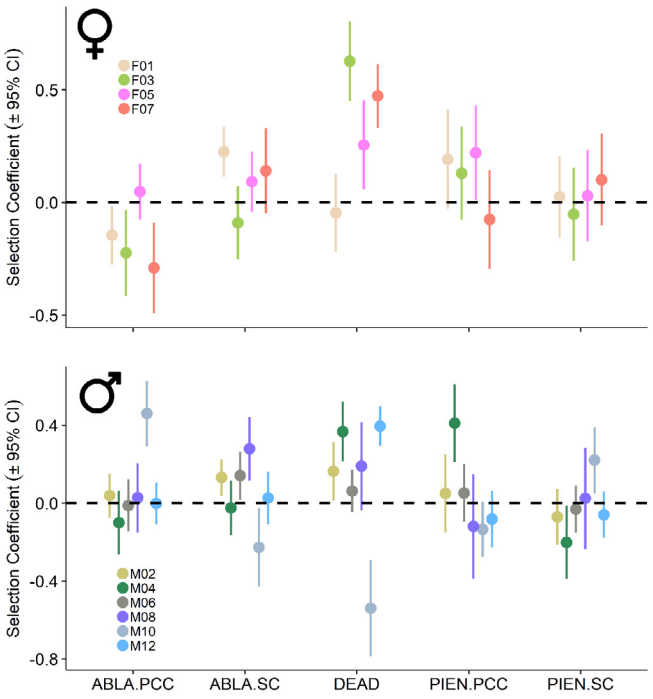


Fig. 3. Standardized selection coefficients (± 95% CIs) derived from our winter step-selection functions for individual female (top panel) and male (bottom panel) Canada lynx (*Lynx canadensis*) in spruce beetle (*Dendroctonus rufipennis)*-impacted forests of southwestern Colorado, USA. The dashed line at 0 indicates no selection or avoidance. Forest metrics were quantified from remotely sensed variables using methods developed by Savage et al. (2017). Covariate codes ABLA, PIEN, and DEAD indicate subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and percent total tree mortality in the canopy, respectively. The code PCC indicates percent canopy cover and code SC indicates subcanopy tree count.

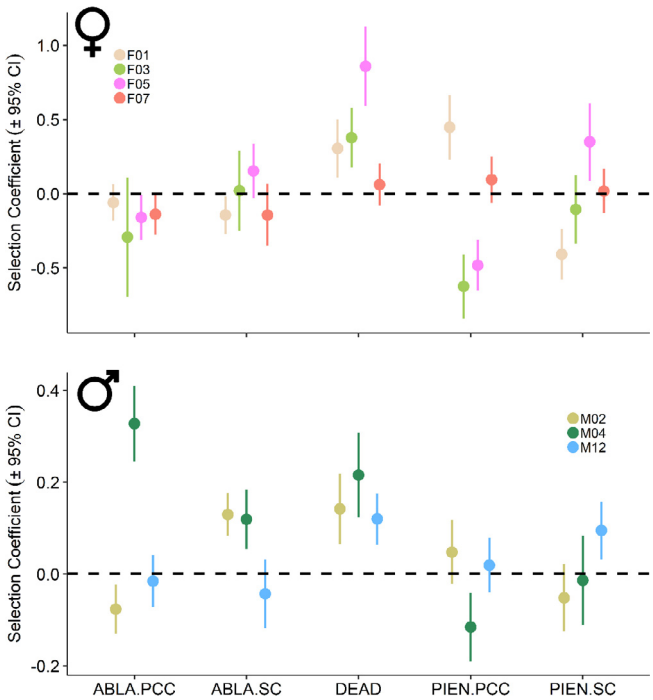


Fig. 4. Standardized selection coefficients (± 95% CIs) derived from our summer step-selection functions for individual female (top panel) and male (bottom panel) Canada lynx (*Lynx canadensis*) in spruce beetle (*Dendroctonus rufipennis)*-impacted forests of southwestern Colorado, USA. The dashed line at 0 indicates no selection or avoidance. Forest metrics were quantified from remotely sensed variables using methods developed by Savage et al. (2017). Covariate codes ABLA, PIEN, and DEAD indicate subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and percent total tree mortality in the canopy, respectively. The code PCC indicates percent canopy cover and code SC indicates subcanopy tree count.

for areas with larger-diameter dead Engelmann spruce trees (Table 3).

Finally, Canada lynx exhibited clear patterns of selection at our finest scale of selection along movement paths (fourth-order selection). Male and female lynx, regardless of season, tended to move toward areas with more dead canopy cover than expected given random availability along movement paths (Figs. 3 and 4). This movement pattern was consistent with selection at the broader landscape- and home-range scales, and reinforced the importance of beetle-impacted areas for Canada lynx use. Similarly, most females and males exhibited selection along movement paths for areas with abundant subalpine fir in the subcanopy during the winter. However, despite some consistent patterns, there was also substantial individual and seasonal variation in movement behavior (Figs. 3 and 4). For instance, the one male lynx (M10) that moved away from areas with more subalpine fir in the subcanopy during the winter months also strongly selected for areas with abundant subalpine fir in the canopy (more so than any other male; Fig. 3). In addition, most females during the winter months selected areas with higher Engelmann spruce in the canopy, whereas in the summer there was much more heterogeneity, with females F03 and F05 avoiding Engelmann spruce canopy cover (Figs. 3 and 4).

3.2. Predictive performance of landscape RSF models and habitat suitability mapping

Top models (both winter and summer) characterizing Canada lynx resource selection at the landscape-scale were predictive of lynx habitat use based on our two evaluations. In the leave-one out validation, we were able to predict the withheld individual lynx use to a high degree based on resource selection patterns of the remaining lynx; the Spearman's rank correlation coefficient (r_s) for winter and summer were r_s = 0.90 (SD = 0.23), and r_s = 0.92 (SD = 0.07), respectively. Furthermore, our 10% withheld sample of GPS locations for each lynx validated well on our putative habitat suitability maps. The Spearman's rank correlation coefficients for winter and summer were high: winter r_s = 0.99 (p < 0.001), summer r_s = 0.99 (p < 0.001). Therefore, we felt confident to use our top RSF models to generate habitat suitability maps for Canada lynx across our beetle-impacted landscape, which we categorized into 10 equal-area bins (Fig. 5).

To establish our binary map, we assessed how many equal-area bins were required to reach a threshold of 95% cumulative lynx use from our withheld GPS locations. For our winter habitat suitability map, we reached 95% use incorporating 5 equal-area bins (bins 6–10; Fig. 6). However, we reached 95% cumulative lynx use including only 4 bins for our summer map (bins 7–10). We classified these areas capturing 95% cumulative lynx use as 'selected' whereas the remaining area was classified as 'less selected' (Fig. 6).

3.3. Functional responses in habitat use across home ranges

We observed consistent positive selection (i.e., use always greater than availability) for horizontal cover, but diminishing strength of selection (relative to the diagonal, proportional use line) as cover increased in home ranges. This same general relationship was seen with live canopy cover of Engelmann spruce and tree size of subalpine fir (Fig. 7; Appendix C). These functional responses indicated that lynx increasingly selected areas with higher horizontal cover, more live canopy cover of Engelmann spruce, and larger subalpine fir trees as these resources became less available within lynx home ranges; or conversely, became less selective as these resources became more available within a home range. Lynx also, during winter, demonstrated a similar

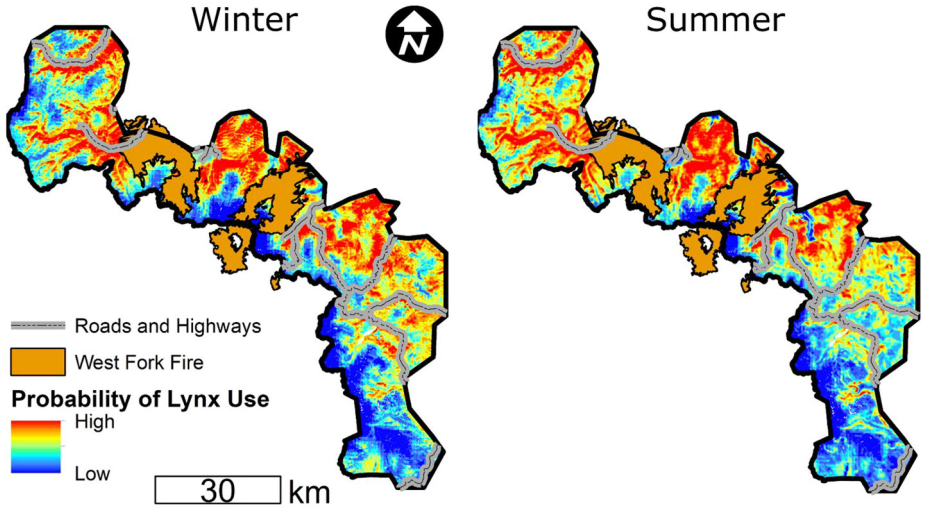


Fig. 5. Predicted relative probability of use for Canada lynx (*Lynx canadensis*) in spruce beetle (*Dendroctonus rufipennis)*-impacted forests of southwestern Colorado, USA. Maps were generated from our top resource selection functions (RSF) at the landscape scale (second-order selection; Johnson 1980) during winter and summer.

functional response for the size of beetle-killed trees (Fig. 7), indicating they increasingly selected for larger-diameter beetled-killed trees when smaller dead trees were more available in home ranges (Fig. 7; Appendix C). Further, lynx exhibited patterns of additive use and consistent selection for relative density of snowshoe hares, tree density of subalpine fir 7.6–12.4 cm (3–4.9 in.) in diameter, and tree size of quaking aspen. Additive use and consistent selection was a situation where lynx exhibited additive use (intercept was greater than 0 and thus above the 1:1 proportional use), but the slope did not differ from 1 as availability increased (Appendix C). The remaining two responses for lynx during winter, which were associated with tree density of Engelmann spruce 12.7–22.6 cm (5–8.9 in.) in diameter and the basal area of dead trees, were more variable and less conclusive than the other responses (Appendix C). In summer, we observed only one significant response of lynx to forest characteristics, which (similar to winter) indicated lynx increasingly selected areas with higher horizontal cover when horizontal cover was less available within their home ranges (Fig. 8; Appendix C). This response also highlighted that lynx consistently selected for higher horizontal cover than expected given availability. The remaining responses did not statistically deviate from proportional habitat use (Fig. 8).

4. Discussion

Our overarching goal was to provide conservation tools that identified the conditions where management actions within spruce beetle-impacted forests could occur without impacting the resource requirements of a federally-listed species – the Canada lynx. Prior to beetle impacts, Canada lynx in the Southern Rocky Mountains generally occupied mature spruce-fir forests dominated by older trees (i.e., 200–350 years old) with live canopy cover where some trees exceeded 600 years in age (Ryerson et al., 2003; Whipple and Dix, 1979). Over the last 600 years in the San Juan Mountains of southern Colorado, western spruce budworm (*Choristoneura occidentalis*) outbreaks were regionally synchronous at 25- to 40-yr intervals with larger events at 83-yr intervals (Ryerson et al., 2003). However, spruce bark-beetles created a novel landscape for the management of this reintroduced lynx population by removing the live canopy about 8–10 years (≈ 2007 initial outbreak) before our study began (2015–2017). This disturbance was unprecedented to the land managers and silviculturists responsible for managing lynx habitat in the Southern Rockies.

We demonstrated that Canada lynx in beetle-impacted forests selected home ranges, use-areas within home ranges, and movement paths in forests with higher tree mortality and generally larger diameter trees than expected under random conditions. This discovery was in contrast to our initial prediction and to previous research in the northern Rocky Mountains in terms of the importance of mature, live forest structures (Holbrook et al., 2019b; Kosterman et al., 2018; Squires et al., 2010). However, our first prediction was more supported at a finer resolution based on field data collected at lynx locations within home ranges. Here, lynx more generally selected forests with greater live components of subalpine fir and live canopy of Engelmann spruce. Our second prediction was generally supported across scales in that lynx selected areas with higher Engelmann spruce-subalpine fir subcanopy at the landscape extent as well as higher horizontal cover within home ranges. Furthermore, Canada lynx exhibited a functional response in habitat use whereby they increasingly selected for attributes such as horizontal cover and live canopy of Engelmann spruce as they became rarer within lynx home ranges. Collectively, this information indicated that: (1) Canada lynx actively use and select forests impacted by spruce bark beetles, especially trees in larger size classes; (2) live trees remaining are important to maintain lynx habitat, and (3) horizontal cover from Engelmann spruce-subalpine fir subcanopy are strongly selected by Canada lynx within the context of spruce-beetle impacted forests. This research provides the first assessment of how Canada lynx, a specialized forest carnivore, navigated a disturbed landscape created by an extensive bark-beetle outbreak. Developing these understandings is particularly timely to conservation science and land management as climate change increasingly alters patterns of disturbance in boreal and subalpine forests.

Our ability to model how Canada lynx responded to disturbance at broad scales required new approaches for mapping forest characteristics in areas severely impacted by spruce beetles (Savage et al., 2017). This approach leveraged the Landsat imagery archive, zero-inflated models, and machine learning to predict percent canopy cover of the 4 dominant conifers on our study area and associated sub-canopies. To construct remotely-sensed maps that accurately depicted tree mortality from beetles at a scale consistent with lynx resource use, Savage et al. (2017) quantified forest metrics in the field on an extensive array of vegetation plots randomly distributed across the beetle-impacted landscape; these plots were central to model building and training. Analyses from Savage et al. (2017) demonstrated that the composition of the surviving subcanopy was heterogeneous and thus critical to consider when evaluating questions associated with wildlife. For example, these maps allowed us to spatially delineate the subcanopies dominated by Engelmann spruce and subalpine fir in stands with high beetle mortality, which were important to Canada lynx at a landscape scale.

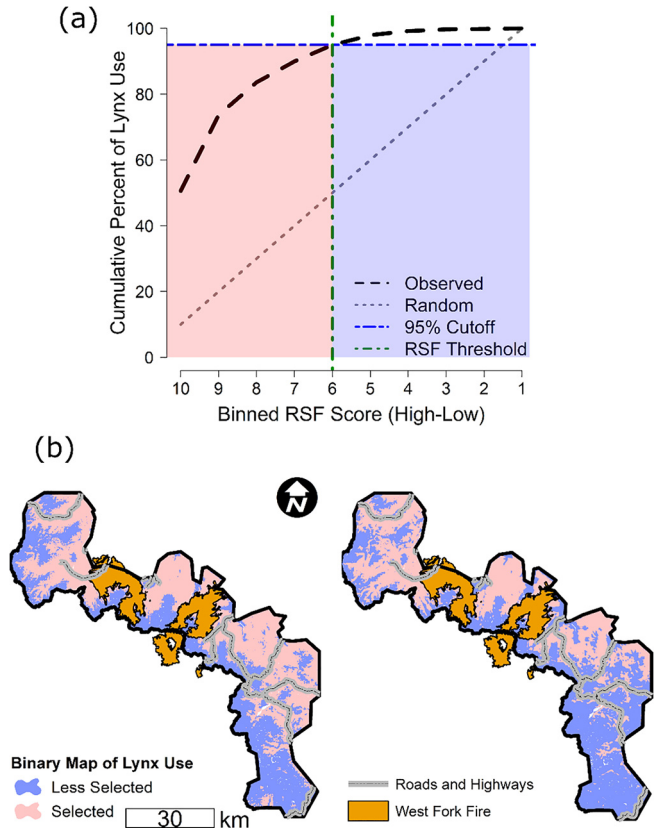


Fig. 6. (a) Cumulative percent of withheld Canada lynx (*Lynx canadensis*) locations across our predicted probabilities of lynx use in spruce beetle (*Dendroctonus rufipennis)*-impacted forests of southwestern Colorado, USA. We generated this using our top landscape-scale resource selection function (RSF) during winter. The x-axis represents 10 equal area RSF bins ranging from high to low relative probability of use. The intersection of the "Observed" curve and the horizontal line indicates the RSF bin that was required to capture 95% of withheld lynx use. The diagonal line indicates the expected curve if withheld lynx locations were randomly distributed across the predicted relative probabilities of lynx-use. The figure indicates the map of predicted lynx-use performed better than random expectation. (b) Based on the results in (a), we generated the binary map of the probability of lynx use during both winter and summer. For instance, in winter areas that were classified as "Selected" (1533 km^2) indicate the RSF scores that captured 95% of the withheld lynx use, whereas areas termed "Less Selected" (1528 km^2) contained the remaining 5% of lynx locations.

Ecologists and forest managers alike are interested in understanding how changes in habitat condition influence the distribution, demography, and resource selection for sensitive species in managed landscapes (Boyce et al., 2002; Johnson, 1980; Leverkus et al., 2018; Thorn et al., 2018). Although resource selection analyses are foundational to our collective understanding of habitat relationships, these studies have well documented and implicit limitations that include: sensitivities to the definition of availability (Beyer et al., 2010; Northrup et al., 2013); confusion in terminology (Lele et al., 2013); functional responses in habitat use that violate the constant selection assumption (Mysterud and Ims, 1998); or failing to account for influences of competition, density-dependence, and predation on resource selection (McLoughlin et al., 2010; van Beest et al., 2015). We acknowledge the complexity involved in understanding how Canada lynx interact with disturbed landscapes. Our ability to document demographic responses and interspecific relationships of lynx in response to landscape-level disturbance was outside the scope of our study. However, our multistage approach that combined the analytical strengths of resource selection analyses and the resulting predictive maps of lynx use, coupled with functional responses to differing environmental gradients, provided a rigorous construct that evaluated variation in selection across different levels of resource availabilities (Holbrook et al., 2019a, 2019b).

Functional responses that examine how resource use changes across a gradient in availability are helpful to understand the complexities of selection, including the variation of selection behavior across individuals (Beyer et al., 2010; Hebblewhite and Merrill, 2008; Mysterud and Ims, 1998; van Beest et al., 2015). Carnivores have been shown to exhibit functional responses to different classes of forest structure (Holbrook et al., 2017a), prey abundance (Zimmermann et al., 2015), and avoidance from motorized winter recreation (Heinemeyer et al., 2019; Squires et al., 2019). Consistent with our predictions, we documented that Canada lynx in winter exhibited particularly strong positive functional responses for horizontal cover, canopy cover of live Engelmann spruce, and for larger beetle-killed trees (≈ 20 cm in diameter). Similar to lynx in non-disturbed landscapes with live canopy cover (Holbrook et al., 2017a; Ivan and Shenk, 2016; Squires et al., 2010), the consistency and narrow range of use that Canada lynx exhibited for horizontal cover within home ranges impacted by beetle outbreak was striking. In other words, Canada lynx that occupied generally lower quality home ranges with low horizontal cover were highly selective in using patches of high horizontal cover, whereas those lynx with abundant horizontal cover relaxed their selection. Similarly, lynx actively selected forest patches of large-diameter, beetle-killed trees when they were rare in home ranges and used this resource in proportion to availability when abundant. Understanding how selection differs over environmental gradients that vary in availability has important ramifications to timber salvage and other forest management activities in disturbed landscapes.

Salvage logging in disturbed landscapes can reduce biodiversity and therefore may be viewed as inappropriate in protected areas (Thorn et al., 2018). However, complex socio-economic interactions between natural disturbance processes and the desire to promote timber salvage often result in a cascade of ecological and environmental consequences that are poorly understood in actively managed landscapes (Leverkus et al., 2018). Delays in harvesting beetle-killed trees post-disturbance can significantly reduce their value at the mill (Loeffler and Anderson, 2018). This includes the mill value of Engelmann spruce (Vaughan, 2016), the primary tree species impacted by spruce bark-beetles in lynx habitat of the Southern Rockies. Thus, ecologists and managers require tools that balance both the social and economic constraints of tree salvage with the legal and ethical needs to promote sensitive species conservation. The fact that Canada lynx selected higher levels of beetle-killed trees at the landscape and home range scales and exhibited a positive functional response for beetle-killed trees, creates a management challenge relative to tree salvage. Canada lynx also selected home ranges with abundant live spruce-fir trees within beetle-impacted landscapes; areas selected by lynx within home ranges supported approximately 2.5 times the number of live subalpine fir trees from 3 to 8.9 in. DBH (7.6–22.6 cm) compared to areas randomly available.

Managers in the Southern Rockies often must consider the need to reduce fuel loadings in beetle-impacted forest to address a perceived risk of increased fire (Pelz et al., 2015). Mitigation efforts that reduce potential ladder fuels for fires also decrease the high horizontal cover from spruce and fir subcanopies required by lynx and hares. These management actions may also be contrary to current lynx management directions (USDA Forest Service, 2008) and to our observed patterns of selection. Fires in subalpine forests of the Southern Rockies are naturally infrequent, but extensive and stand-replacing events (Sibold et al., 2006) with no indication that recent spruce beetle outbreak has altered fire severity (Andrus et al., 2016). The severity of these fires immediately post-disturbance (< 5 yr) are mostly influenced by weather conditions, topography, and pre-outbreak basal area (Andrus et al., 2016). However, Carlson et al., (2017) found that multiple disturbances in the Southern Rockies such as high-severity spruce beetle outbreaks prior to fire could delay vegetation recovery through complex ecological impacts affecting forest soils, seed sources, and delayed sprouting.

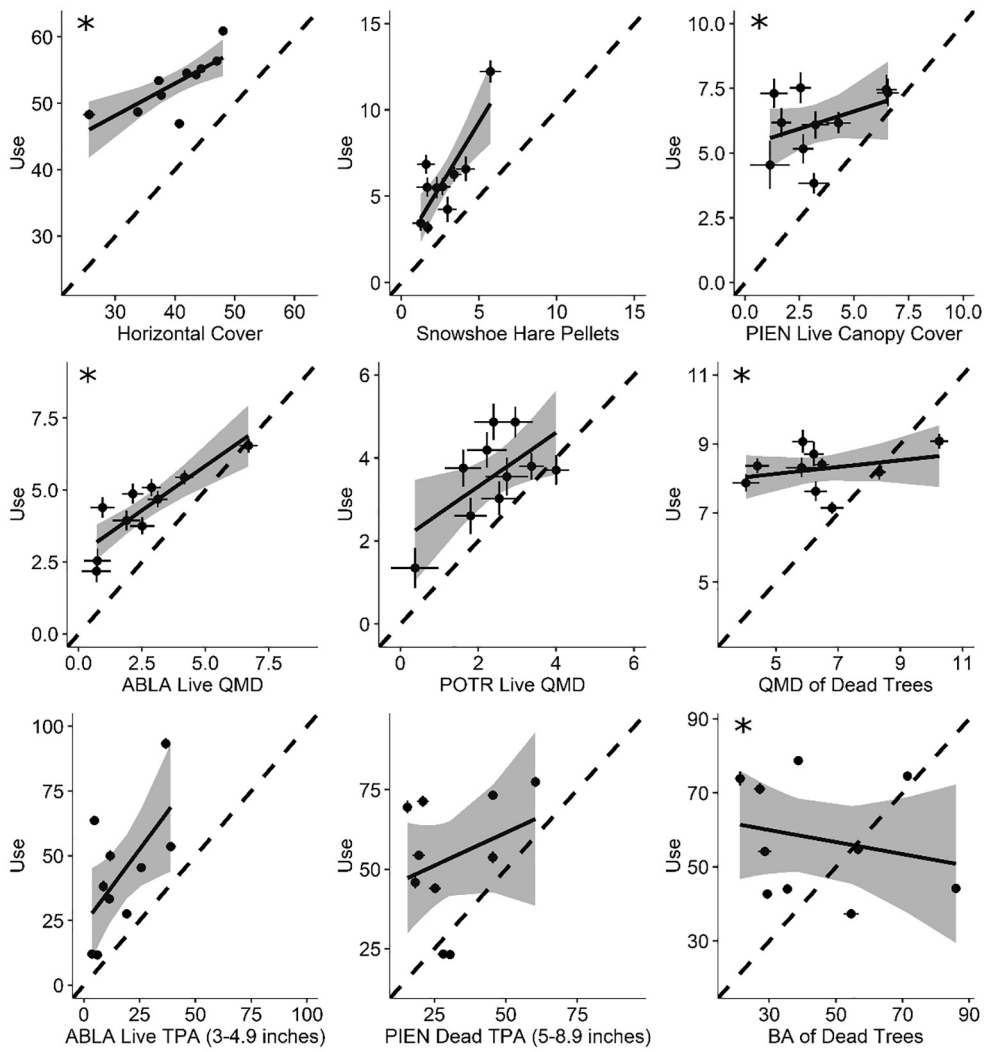


Fig. 7. Functional responses in habitat use during the winter at the home range scale for male and female Canada lynx (*Lynx canadensis*) in spruce beetle (*Dendroctonus rufipennis)*-impacted forests of southwestern Colorado, USA. The diagonal line indicates random (i.e., proportional) habitat use and confidence bounds are 90% CIs. Each data point represents the mean value at used and available locations for each lynx (± 1 SE). An asterisk (*) at the top left indicates the slope ≠ 1, and thus a statistical response ($\alpha = 0.10$). Covariate codes POTR, PIEN, ABLA indicate quaking aspen (*Populus tremuloides*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*), respectively, while QMD, TPA, and BA indicate quadratic mean diameter, trees per acre, and basal area. Covariates were only evaluated if they were included in the top model from the third-order resource selection function.

In the Pacific Northwest, outbreaks of bark beetles and a defoliator species like western spruce budworm (*Choristoneura freemani*) reduced wildfire severity in a manner that could enhance landscape-level resistance to fire impacts (Meigs et al., 2016). Thus, vegetative characteristics of insect-impacted forests that support Canada lynx are in constant flux that change over time and may require additional study. Although our results advance lynx conservation and management in beetle-impacted forests, better mechanistic understandings are needed to best balance conservation planning for Canada lynx with the most pressing forest management and environmental challenges such as long-term fire and fuels management in spruce beetle-impacted forests.

We assumed one important underlying mechanism regarding why Canada lynx preferentially selected forest stands composed of large-diameter and abundant beetle-killed trees with developed live Engelmann spruce-subalpine fir understories was the relationship between high horizontal cover and snowshoe hare abundance (Berg et al., 2012; Hodges, 2000; Ivan et al., 2014; Lewis et al., 2011). In other words, we assumed that high tree mortality in beetle-impacted forest increased the development of subcanopy vegetation, that in turn, increased the density of snowshoe hares. Insect outbreaks can dramatically change the structure and composition of spruce-fir (Veblen et al., 1991) and lodgepole pine-dominated (Amoroso et al., 2013; Pelz et al., 2015) forests for many decades. Spruce and pine beetle outbreaks generally release shade-tolerant understory trees, especially subalpine fir (Carlson et al., 2020; Hawkins et al., 2012; Pelz et al., 2015; Rhoades et al., 2017; Veblen et al., 1991). Dependent on seed sources and site conditions, mountain pine beetle can promote the development of spruce-fir understories (Perovich and Sibold, 2016; Sibold et al., 2007), which could improve some lynx habitat in western Colorado over time. In lodgepole pine forests, understory trees experienced greater annual growth following outbreaks of mountain pine bark beetle for multiple tree species (lodgepole pine, subalpine fir, and Engelmann spruce; Rhoades et al., 2017). Thus, silvicultural prescriptions that protect and promote the restoration of the forest understory dominated by spruce-fir would promote conditions selected by Canada lynx. In Colorado, for example, subalpine fir recruitment was most abundant in uncut, unburned, pine beetle-killed stands compared to stands that received salvage logging or burning after the beetle outbreak (Rhoades et al., 2018). Salvage logging also reduced the growth of lodgepole pine and subalpine fir regeneration following beetle-impacts due to the importance of shade in the development of a spruce-fir understory (Collins et al., 2011). Thus, silvicultural prescriptions for tree salvage that protect and promote the existing spruce and subalpine fir understory and maintain the necessary shading, would be most consistent with conservation of lynx habitat in spruce beetle-impacted forests.

Similar to other populations (Mowat et al., 1996; O'Donoghue et al., 1998; Poole, 1994; Simons-Legaard et al., 2016; Squires and Ruggiero, 2007), snowshoe hares account for the primary biomass of prey for Canada lynx in the Southern Rockies (Ivan and Shenk, 2016). However, snowshoe hare populations occur at low densities (< 1.0 hare/ha) in the Southern Rockies across seasons and forest types (Ivan et al., 2014). Given hare density and survival considerations, managers would favor a

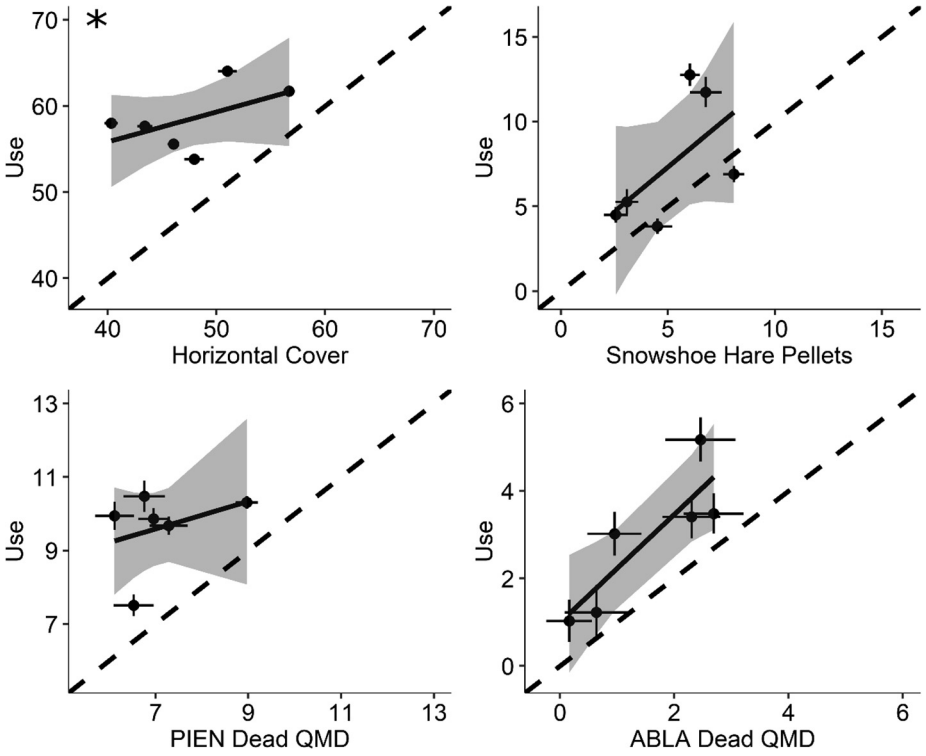


Fig. 8. Functional responses in habitat use during the summer at the home range scale for male and female Canada lynx (*Lynx canadensis*) in spruce beetle (*Dendroctonus rufipennis)*-impacted forests of southwestern Colorado, USA. The diagonal line indicates random (i.e., proportional) habitat use and confidence bounds are 90% CIs. Each data point represents the mean value at used and available locations for each lynx (± 1 SE). An asterisk (*) at the top left indicates the slope ≠ 1, and thus a statistical response ($\alpha = 0.10$). Covariate codes PIEN, ABLA, QMD indicate Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and quadratic mean diameter, respectively. Covariates were only evaluated if they were included in the top model from the third-order resource selection function.

landscape mosaic of mature spruce-fir forests and early lodgepole pine over thinned stands if the goal is to enhance snowshoe hare populations and by extension Canada lynx (Ivan et al., 2014). Mature spruce-fir forests are most valuable to hares in the Southern Rockies due to their temporal persistence and spatial extent of this cover type. Contrary to expectation, patterns of occupancy for snowshoe hares in the Southern Rockies was not materially altered by spruce or mountain pine beetle outbreaks (Ivan et al., 2018). However, red squirrels exhibited the strongest negative response to bark-beetle outbreaks of any species sampled (Ivan et al., 2018), presumably due to their dependence on cone crops (Wheatley et al., 2002). In Colorado, Canada lynx increase their reliance on red squirrels (≈ 70% of diet) during periods of low snowshoe hare density (Ivan and Shenk, 2016). The periods when lynx use of squirrels was high in diets and hare use was low corresponded to when females ceased kitten production for approximately 2 years (Shenk, 2009). Thus, Canada lynx in the Southern Rockies are at greater risk for potentially decades due to their increased vulnerability to reduced hare abundance given much lower red squirrel densities in beetle-impacted forests. Silvicultural prescriptions that encourage spruce-fir understory regeneration for hares in beetle-impacted forests and that also speed the development of cone-bearing trees for red squirrels would further efforts to conserve lynx across the species' range.

5. Conclusion

Our research advances the scientific understandings of Canada lynx habitat-use in spruce-beetle impacted forests and highlighted potential management challenges and opportunities for timber salvage. Our research also provides spatial tools that inform lynx conservation in disturbed landscapes of the Southern Rockies. Resource selection surfaces (continuous and binary) of predicted use by Canada lynx allow managers to distinguish the beetle-impacted landscapes most selected by lynx from those areas of lesser conservation value where tree salvage may have priority. Across spatial scales, we also demonstrated that Canada lynx select forest conditions, such as large-diameter beetle-killed trees in areas of abundant spruce-fir understory and live subalpine fir trees, that potentially conflict with tree salvage depending on implementation strategies and prescriptions. Both lynx and hare depend on the high horizontal cover provided by spruce-fir regeneration, which increase in areas of high tree mortality. However, we recognize the conundrum between forest management that promotes forest subcanopy for a federally listed species, like Canada lynx, with the need to use mechanical or fire treatments every 20 years to reduce fuel loads and perceived fire risk (Pelz et al., 2015). Ecologically, these interventions are outside the range of natural variation in boreal forests of the Southern Rockies and are only practical in areas of particularly high resource or infrastructure value, or to promote human safety (Pelz et al., 2015). This challenge is especially acute in this new era of "megadisturbances" that threaten the boreal and subalpine forests (Gauthier et al., 2015; Millar and Stephenson, 2015; Price et al., 2013; Sherriff et al., 2011) required by both forest-dependent species and forest-product based communities. Thus, in the Southern Rockies, the management of Canada lynx in the spruce-beetle impacted forests would include silvicultural prescriptions that provide forest structures and compositions that are central to the species' resource selection. These actions could occur in spatially targeted areas that balance the regions of highest conservation value with approaches that also facilitate timber salvage in an ecosystem that is dominated by infrequent, stand-replacing fire events (Sibold et al., 2006), and where short term (< 5 yr) fire severity is largely driven through complex interactions of weather conditions, topography, and pre-outbreak basal area (Andrus et al., 2016).

CRediT authorship contribution statement

John R. Squires: Conceptualization, Methodology, Investigation, Funding acquisition, Writing draft. **Joseph D. Holbrook:** Conceptualization, Methodology, Formal analysis, Writing draft. **Lucretia E. Olson:** Conceptualization, Methodology, Editing. **Jacob S. Ivan:** Conceptualization, Methodology, Investigation, Editing. **Randal W. Ghormley:** Conceptualization, Methodology, Investigation, Editing. **Rick L. Lawrence:** Conceptualization, Methodology, 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 material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118400.

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