Forest Ecology and Management 422 (2018) 114–124

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Spatio-temporal responses of Canada lynx (*Lynx canadensis*) to silvicultural treatments in the Northern Rockies, U.S.

Joseph D. Holbrook[a,b,*], John R. Squires[a], Barry Bollenbacher[c], Russ Graham[d], Lucretia E. Olson[a], Gary Hanvey[c], Scott Jackson[e], Rick L. Lawrence[b]

[a] *USDA Forest Service, Rocky Mountain Research Station, 800 East Beckwith Ave., Missoula, MT 59801, USA*
[b] *Department of Land Resources and Environmental Sciences, Montana State University, PO Box 173120, Bozeman, MT 59717, USA*
[c] *USDA Forest Service, Region 1, 26 Fort Missoula Rd., Missoula, MT 59804, USA*
[d] *USDA Forest Service, Rocky Mountain Research Station, 1221 South Main St., Moscow, ID 83843, USA*
[e] *USDA Forest Service, National Carnivore Program, 26 Fort Missoula Rd., Missoula, MT 59804, USA*

ARTICLE INFO

Keywords:
Endangered species
Functional response
Hurdle model
Intensity of use
Lepus americanus
Multi-scale
Occupancy
Patch use
Resource selection
Silviculture
Snowshoe hare

ABSTRACT

Forest managers are often tasked with balancing opposing objectives, such as altering forest structure and conserving forest-dwelling animals. Consequently, to develop holistic strategies managers require information on how forest manipulations influence species of conservation concern, particularly those that are federally threatened or endangered. Here, we characterized how differing silvicultural treatments ($n = 1,293$ – forest thinnings; removal of small trees, selection cuts; trees harvested in small patches, and regeneration cuts; clearcuts of nearly all trees) influenced the resource use of a threatened forest carnivore, Canada lynx (*Lynx canadensis*), over a temporal gradient of 1–67 years after treatment. To do this, we used an extensive GPS dataset on 66 Canada lynx (i.e., 164,593 locations) collected during 2004–2015 within the Northern Rocky Mountains, U.S. We used univariate analyses and hurdle regression models to evaluate the spatio-temporal factors influencing lynx use of treatments. Our analyses indicated that Canada lynx used treatments, but there was a consistent cost in that lynx use was low up to ~10 years after all silvicultural actions. However, cumulative use (in both winter and summer) by lynx reached 50% at ~20 years after a thinning treatment, whereas it took ~34–40 years after a selection or regeneration cut. This indicated that Canada lynx used thinnings at a faster rate post-treatment than selection or regeneration cuts, and that lynx used selection and regeneration cuts in a similar fashion over time. Further, we discovered that lynx occupancy and intensity of treatment use was influenced by the composition of forest structure in the surrounding neighborhood. In some instances, the existing forest structure surrounding the treatment and the time since treatment interactively influenced lynx use; a pattern characterizing a spatio-temporal functional response in habitat use. This demonstrated that both the recovery time as well as the spatial context of a particular area are important considerations when implementing different silvicultural treatments for Canada lynx at the landscape scale. For example, if a selection cut was implemented with abundant mature, multi-storied forest (i.e., a preferred habitat by lynx) in the surrounding landscape, lynx would use these treatments less over time than if the neighborhood contained less mature forest. Forest managers can apply our spatio-temporal understandings of how lynx respond to forest silviculture to refine expectations and develop strategies aimed at both forest management and the conservation of Canada lynx.

1. Introduction

Forest managers, and in particular those of public lands, are increasingly faced with the challenge of balancing opposing objectives. For instance, in the forests of North America a pervasive challenge is the conservation of threatened and endangered species that rely on complex forest structures, while simultaneously managing disturbance (e.g., wildfire risk, bark beetle outbreaks) or forest products through silviculture (e.g., Zielinski et al., 2013; Stephens et al., 2014; Tempel et al., 2014; Sweitzer et al., 2016). Unfortunately, the difficulty of navigating these issues has only increased in recent decades given the increase in forest disturbances such as wildfire and bark beetle outbreaks (e.g., Westerling et al., 2006; Bentz et al., 2010; Jones et al., 2016). Balancing species conservation and managing forest

---

* Corresponding author at: USDA Forest Service, Rocky Mountain Research Station, 800 East Beckwith Ave., Missoula, MT 59801, USA.
E-mail address: jholbrook03@gmail.com (J.D. Holbrook).

https://doi.org/10.1016/j.foreco.2018.04.018
Received 7 February 2018; Received in revised form 6 April 2018; Accepted 7 April 2018

2.2. Silvicultural treatments, surrounding forest structure, and treatment use by Canada lynx

2.2.1. General overview of analysis

Our main objective was to characterize how time since treatment, treatment type, and surrounding forest structure influenced treatment use by Canada lynx. Given the diversity of silvicultural treatments within lynx home ranges, we first developed an ecologically-based framework to stratify treatments. We used the U.S. Forest Service's FACTS (Forest Activity Tracking System) database and a time-series (1972–2014) of the Normalized Burn Ratio (NBR), a variable created from the Landsat archive using the near infrared (NIR) and shortwave infrared (SWIR) bands (i.e., NBR = NIR − SWIR/NIR + SWIR), to identify distinct silvicultural treatments and evaluate the response of vegetation as a function of time since treatment. The NBR is similar to the Normalized Difference Vegetation Index (NDVI = NIR − Red/NIR + Red), but previous work has demonstrated that NBR outperforms NDVI when assessing differences in vegetation impact (e.g., Escuin et al., 2008; Harris et al., 2011). For instance, the gradient of the NBR was 1.6–2.3 times wider than the gradient of NDVI for the same areas impacted by wildfire (Escuin et al., 2008; Harris et al., 2011), which highlighted the increased resolution of the NBR to discern differences in vegetation responses. Therefore, we used the NBR to validate our treatment stratification from FACTS, which we expected to capture a gradient in vegetation impact. We then used this stratification, along with univariate analyses and hurdle regression models (Mullahy, 1986; Zeileis et al., 2008), to address spatio-temporal questions concerning treatment use (i.e., both occupancy and intensity of use) by Canada lynx. Our application of hurdle models was similar to evaluations of patch occupancy and intensity of use for woodland caribou (*Rangifer tarandus caribou*) in residual forest stands (Lesmerises et al., 2013).

2.2.2. Canada lynx data

We used a dataset of GPS locations (164,593 locations; Fig. 1) from Canada lynx that occupied managed landscapes to assess their use of silvicultural treatments. During 2004–2015, we captured and equipped 66 lynx with store-on-board GPS units (Lotek Wireless, Newmarket, Ontario, Canada or Sirtrack Ltd., Havelock North, New Zealand). Our capture efforts were approved by the Institutional Animal Care and Use Committee (University of Montana IACUC permits 4–2008 and TE053737–1). We programmed GPS collars to collect a location every 30 min for 24 h every other day for the life of the collar (generally 6–8 months). Spatial accuracy of locations averaged 30 m as reported by Squires et al. (2013) and fix rate was approximately 86% (see Holbrook et al., 2017a for additional details on GPS data processing). We assessed occupancy and intensity of use of treated patches across seasons, which we defined as summer (April – October) and winter (November – March).

2.2.3. Stratifying silvicultural treatments with the Normalized Burn Ratio

We used the U.S. Forest Service's FACTS database to identify different silvicultural treatments that occurred within Canada lynx home ranges (home ranges defined in Holbrook et al., 2017a). The FACTS database is a patch-based geospatial layer of silvicultural actions with records going back to the 1920s. Although useful for many research applications (e.g., see applications of FACTS in Zielinski et al., 2013; Tempel et al., 2014; Sweitzer et al., 2016), FACTS data suffers from spatio-temporal errors in terms of treatment extent within polygons and timing of implementation. Therefore, while others have assumed differences among treatment strata derived from FACTS, we implemented a novel assessment to validate our stratification using a time-series of the NBR.

We used the FACTS database to develop an initial set of six forest treatments, which were composed of 25 unique silvicultural activity types (Appendix A: Table A.1). The six silvicultural treatments included: (1) group selection cut (*n* = 11; trees harvested in small patches usually less than 1 ha and regenerated naturally or by planting), (2) liberation cut (*n* = 60; overstory or competing trees removed moved to liberate subject trees), (3) improvement cut (*n* = 85; removing trees from all size classes as to improve the residual tree quality and growth rates), (4) precommercial thinning (*n* = 346; thinning small trees ~15 cm as to modify species composition and provide growing space for residual trees), (5) regeneration cut with natural regeneration (*n* = 360; clearcut resulting in the remove all or the majority of high forest cover as to regenerate a stand from seed), (6) regeneration cut with planting (*n* = 431; clearcut resulting in the removal of all or the majority of high forest cover and plant trees). We expected regeneration cuts to represent the most severe impact to vegetation followed by selection cut, liberation cut, improvement cut, and precommercial thinning; a total of 1,293 treated patches (i.e. silvicultural cuts or thinnings) were included in this analysis. We only considered patches that were modified through a single action (i.e., we excluded patches with multiple treatment actions) and we discarded any patches that were affected by wildfires.

To evaluate vegetation impact and recovery we assessed how the NBR changed as a function of treatment type and time since treatment. We developed the time-series of NBR for our study area using the Landsat archive as part of the time-series analysis in Savage et al. (2018). We calculated the mean NBR across all treatment patches for each year since treatment (starting at year *t*-1). We then evaluated how mean NBR (± 90% CIs) for each year and treatment changed as a function of time since treatment. For this analysis, our temporal gradient ranged up to 39 years after a treatment. Our premise was that if the silvicultural treatments created distinct vegetation conditions after a harvest, the trajectory of vegetation recovery (indexed via NBR) would differ by treatment type. We used program R (R Core Team, 2017) to complete these analyses.

Our initial assessment of the NBR across time since treatment indicated there were some natural groupings among different treatment types (Fig. 2a). For instance, liberation cuts and group selection cuts, as well as improvement cuts and precommercial thinnings, generated similar NBR trajectories (Fig. 2a). Therefore, we reclassified our treatments into the following strata (Appendix A:Table A.1): (1) regeneration cuts (combined regeneration cut with natural regeneration and regeneration cut with plantings; *n* = 791), (2) selection cuts (combined group selection and liberation cut; *n* = 71), and (3) thinnings (combined improvement cut and precommercial thinning; *n* = 431). We then repeated our NBR analyses with these combined strata, which demonstrated the distinct patterns of vegetation change across these three groups (Fig. 2b). Consequently, we used these three treatments as our final suite of silvicultural actions (regeneration cut, selection cut, and thinning), which captured a low (e.g., thinning) to high (e.g., regeneration cut) gradient in treatment severity.

In order to ensure that our treatment stratification was relevant to Canada lynx ecology, we calculated the range of NBR at GPS locations for all lynx (*n* = 64 lynx, 63,204 locations) sampled during the winter season. We used the winter season because winter is when lynx exhibit more specificity in habitat selection (Squires et al., 2010; Holbrook et al., 2017a). Based on previous work highlighting the disproportionate use of mature forest structures by lynx (Squires et al., 2010; Holbrook et al., 2017a), we expected lynx to use a high value and narrow range of the NBR, indicative of recovered vegetation. We calculated a mean NBR (from 2013) for each lynx and subsequently calculated the interquartile range (IQR). We then evaluated how the IQR related to the NBR trajectories associated with our three silvicultural treatments (Fig. 2b). Consistent with our hypothesis, Canada lynx used a high value and narrow range of the NBR (lynx IQR in Fig. 2b) indicating that our stratification of silvicultural treatments was relevant to lynx.

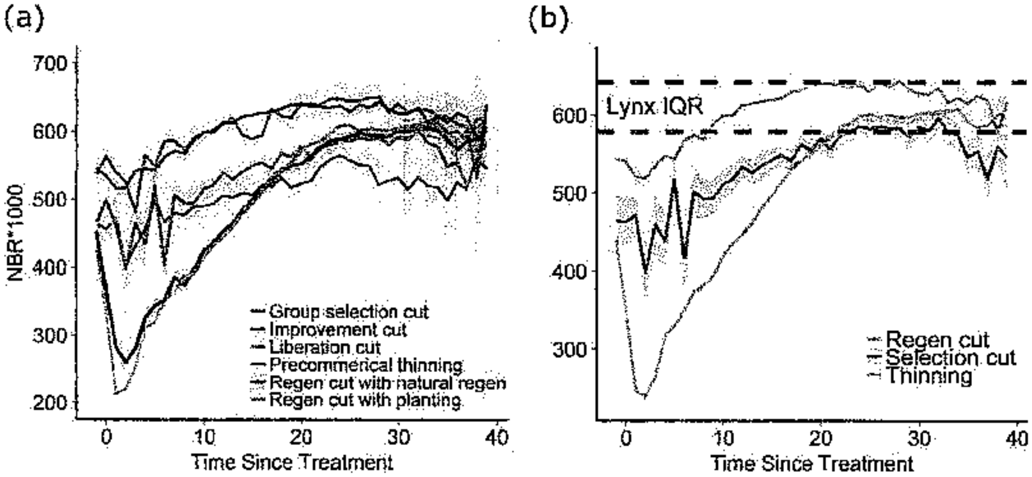

Fig. 2. Mean (± 90% CIs) Normalized Burn Ratio (NBR) * 1000 per year for each treatment type across a gradient in time since treatment (starting at year t-1) during 1972–2014 (i.e., 1–39 years post-treatment) for our potential suite (a) as well as our final set of treatments (b). Horizontal lines in (b) represent the interquartile range of NBR at GPS locations averaged for 64 Canada lynx (*Lynx canadensis*) during the winter season. Regen indicates regeneration.

2.2.4. *Evaluating Canada lynx use of silvicultural treatments*

With our silvicultural treatments identified, we then evaluated our main questions concerning how time since treatment and the surrounding forest structure influenced patch occupancy and intensity of use by Canada lynx during winter and summer (see Fig. 3). Patch occupancy was defined as the presence of a GPS location within a silvicultural treatment, while the intensity of use was defined as the number of GPS locations within a silvicultural treatment (i.e., for all patches that were occupied). For each treated patch within Canada lynx home ranges, we calculated the patch size (m^2) and the number of lynx locations within the patch.

We buffered each treatment by 1.5 and 4 km (e.g., Fig. 3), which corresponded to the 95th percentile of hourly movement rates by Canada lynx and the radius of median home range sizes of lynx reported in Holbrook et al. (2017a). We calculated the proportion of forest structural stages (e.g., Fig. 3) within each buffer using the mapped predictions (~80% classification accuracy) from Savage et al. (2018). Forest structural stages included: (1) stand initiation (e.g., ~0–8 years after disturbance with few large trees remaining), (2) sparse forests (e.g., naturally sparse or mechanically thinned, and generally ~9–25 years after modification), (3) advanced regenerating forests (e.g., generally ~25–40 years old with dense horizontal and vertical cover), and (4) mature forests (e.g., multi-storied stands generally ≥ 40–50 years old with dense horizontal and vertical cover). Holbrook et al. (2017a) quantified the differences among these four structural stages in much greater detail using Forest Inventory and Analysis data (see Holbrook et al., 2017a). We used the 1.5 and 4 km buffers simply to identify the scale that fit the data best; the proportion of forest structural stages were highly correlated across scales ($r \geq 0.74$) and thus captured similar variation.

Not all treated patches were sampled equally by lynx throughout a home range. Therefore, we counted the number of GPS locations outside of the treated patch but within the 4 km buffer, which served as an index of treatment-level sampling intensity by lynx. In addition, for every treated patch we developed a time since treatment variable by finding the median year of the lynx GPS locations within the 4 km buffer and subtracting it from the year of treatment. Collectively, these data generated a suite of five explanatory variables (some of which were summarized at two scales; 1.5 and 4 km^2) and two response variables (Table 1). We used ArcGIS (ESRI, 2011) and the Geospatial Modelling Environment (Beyer, 2012) to develop our suite of variables.

The patch size of a treatment as well as the sampling intensity by

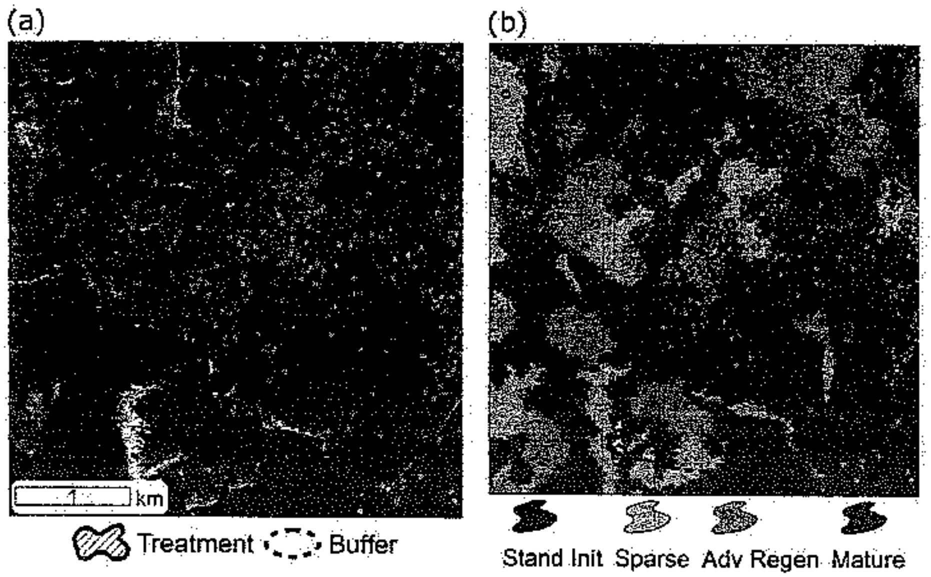

Fig. 3. Example of our sampling scheme to understand how silvicultural treatments, time since treatment, and surrounding forest structure influenced patch occupancy and intensity of use by Canada lynx (*Lynx canadensis*). Dots indicate lynx GPS locations. Panel (a) shows that a regeneration cut from 1979 was occupied (i.e., at least 1 location in treatment) and intensely used (i.e., 17 total locations in treatment) by Canada lynx. Panel (b) shows the distribution of forest structural stages outside of the treatment but inside the buffer or neighborhood. Abbreviations Stand Init and Adv Regen indicate stand initiation and advanced regeneration, respectively.

Table 1
General summary of variables (across treatment types: regeneration cut, selection cut, and thinning) used to evaluate how silvicultural treatment influenced patch use by Canada lynx (*Lynx canadensis*).

Variable	Description	Extent	Mean (Range)
Response	Presence/Absence of a GPS location	Patch-level	NA; binary variable
	Count of GPS locations	Patch-level	Winter: 5 (0–215) Summer: 7 (0–417)
Offset components	Patch size	Patch-level	12 ha (0.40–167 ha)
	GPS locations in 4 km neighborhood	4 km neighborhood	Winter: 1,149 (1–5,327) Summer: 1,850 (1–8,102)
Explanatory	Time since treatment	Patch-level	32 yrs (1–67 yrs)
	Proportion stand initiation	1.5 and 4 km neighborhood	1.5 km: 0.04 (0.00–0.50)[†] 4 km: 0.05 (0.00–0.40)[†]
	Proportion sparse	1.5 and 4 km neighborhood	1.5 km: 0.21 (0.02–0.78)[†] 4 km: 0.24 (0.07–0.67)[†]
	Proportion advanced regeneration	1.5 and 4 km neighborhood	1.5 km: 0.18 (0.01–0.52)[†] 4 km: 0.16 (0.02–0.67)[†]
	Proportion mature	1.5 and 4 km neighborhood	1.5 km: 0.57 (0.08–0.91)[†] 4 km: 0.54 (0.08–0.79)[†]

[†] Values were similar for summer and winter.

lynx in the 4 km buffer could influence the probability of occupancy and intensity of patch use by Canada lynx (e.g., larger patches sampled more intensely within the 4 km buffer are likely to be used more; Lesmerises et al., 2013). Therefore, we incorporated the sampling intensity and the patch size of a treatment as a correction, or an offset in our regression analyses, for our measures of patch occupancy and intensity of use (Table 1). For our initial assessments of the intensity of use by lynx, we applied the following equation:

$$\textit{Intensity of Use} = \frac{\textit{Number of GPS locations in a patch}}{\log(\textit{Number of GPS locations in 4 km buffer} \times \textit{Patch size})}$$

For all analyses, we only evaluated treated patches that were sampled by lynx (i.e., at least 1 GPS location in the 4 km buffer). Thus, all treatments were generally accessible to lynx and our analyses were approximately at the third-order of resource use (Johnson, 1980).

We initially assessed how the intensity of use by lynx was distributed across our gradient in time since treatment. Because of the heterogeneity in sampling intensity by lynx, we used the maximum intensity of use for each year across our time since harvest gradient. Next, we assessed differences in the temporal distribution of lynx use across the different silvicultural treatments, which only included the patches occupied by Canada lynx (i.e., ≥1 GPS location within a treated patch). We used an analysis of variance (ANOVA) to evaluate if time since treatment for the patches occupied by lynx differed between regeneration cuts, selection cuts, and thinnings ($\alpha = 0.05$). If we documented differences, we calculated 95% confidence intervals of time since treatment to determine the direction and magnitude of the differences. Lastly, we assessed how the cumulative proportion of lynx use varied across time since treatment, which provided a more refined comparison of intensity of lynx use between treatments. We predicted that treatment use by Canada lynx would be distributed earlier after a softer treatment (e.g., thinnings) and later after a harsher treatment (e.g., regeneration and selection cuts).

To evaluate what multivariate factors influenced treatment use by Canada lynx, we used hurdle regression models (Mullahy, 1986; Zeileis et al., 2008) and an information-theoretic approach (Burnham and Anderson, 2002). Similar to Lesmerises et al. (2013), we used hurdle models because they are efficient when dealing with overdispersed data and a large number of zeros. We observed many patches that were sampled by lynx (i.e., GPS locations within the 4 km buffer), but contained no lynx locations within the treated patch itself. In addition, hurdle models account for both a binary process (i.e., patch occupancy) and a count process (i.e., intensity of patch use), which facilitates a more refined assessment of patch use by lynx. Specifically, the zero hurdle model (Binomial distribution with a logit link) considers the entire dataset but censors all counts (i.e., $y \geq 1$) to $y = 1$, while the count model (Negative Binomial distribution with a log link in our case) only considers treated patches with at least 1 lynx location (i.e., left truncated at $y = 1$; Zeileis et al., 2008).

Prior to developing hurdle models, we performed preliminary assessments to ensure appropriate model building. First, as aforementioned, we specified an offset term in our hurdle models: log(number of GPS locations in 4 km buffer × patch size). Second, for each treatment and season we identified the most supported scale (either 1.5 or 4 km) for our neighborhood metrics (Table 1, Fig. 3) using Akaike's Information Criterion corrected for sample size (AIC_c). Finally, we assessed collinearity among the remaining covariates and removed those that were contributing to high correlations ($|r| > 0.60$). This resulted in the removal of sparse forest metrics from all models because it was correlated with mature forest.

We developed our candidate models for each treatment and season to evaluate the following predictions concerning how time since treatment and the surrounding forest structure influenced patch use by Canada lynx:

1. Time since treatment would be more influential for patch use of severe treatments (e.g., regeneration cuts) relative to softer treatments (e.g., thinning) because Canada lynx avoid forests with mostly open canopies (Malentzke et al., 2008; Squires et al., 2010; Holbrook et al., 2017a). In addition, we expected the influence of time since harvest to be more pronounced during the winter because lynx increase their use of mature, older stands (Squires et al., 2010; Holbrook et al., 2017a).
2. A neighborhood of largely mature and advanced regenerating forest would likely decrease patch use by Canada lynx because lynx preferentially use mature and advanced regeneration structural stages (Holbrook et al., 2017a). This prediction describes context-dependent patch use, which is a functional response in habitat use (e.g., Mystrud and Ims 1998).
3. Finally, the influence of forest structure within the neighborhood of a silvicultural treatment could depend on how long ago the treated patch was harvested. In other words, time since treatment could interact with the amount of mature or advanced regenerating forest within the neighborhood to influence patch use by Canada lynx. This prediction describes a spatio-temporal functional response in habitat use by integrating time (i.e., time since treatment) with the spatial composition of forest structure in the neighborhood.

Table 2
Model selection table containing ΔAIC_c values (AIC_c weights) for each hurdle model evaluated characterizing how silvicultural treatment influenced patch use by Canada lynx (*Lynx canadensis*). We evaluated models for regeneration cuts, selection cuts, and thinning during the winter and summer season. Bold values indicate selected models. TST indicates time since treatment, Adv Regen indicates advanced regeneration, and Stand Init indicates stand initiation. As a measure of fit, we calculated the Pearson's *r* correlation between observed and expected counts (for all counts greater than 0) using the top model.

Model description	Regeneration cut		Selection cut		Thinning	
	Winter ($n = 1,378$)	Summer ($n = 1,405$)	Winter ($n = 223$)	Summer ($n = 221$)	Winter ($n = 416$)	Summer ($n = 422$)
Null	92.07 (0.00)	10.93 (0.00)	19.34 (0.00)	5.05 (0.02)	19.68 (0.00)	21.21 (0.00)
TST	**0.00 (0.49)**	8.26 (0.01)	5.13 (0.06)	0.02 (0.27)	21.38 (0.00)	24.12 (0.00)
TST + Adv Regen	2.45 (0.15)	5.28 (0.03)	6.67 (0.03)	**0.00 (0.27)**	15.52 (0.00)	13.51 (0.00)
TST + Adv Regen + TST * Adv Regen	4.44 (0.05)	**0.00 (0.44)**	7.88 (0.01)	3.04 (0.06)	19.07 (0.00)	15.32 (0.00)
TST + Mature	3.37 (0.09)	10.81 (0.00)	3.23 (0.14)	3.36 (0.05)	18.12 (0.00)	16.86 (0.00)
TST + Mature + TST * Mature	7.28 (0.01)	12.37 (0.00)	**0.00 (0.73)**	7.22 (0.01)	20.24 (0.00)	17.57 (0.00)
TST + Adv Regen + Mature	5.08 (0.04)	8.76 (0.01)	7.21 (0.02)	3.83 (0.04)	16.61 (0.00)	0.46 (0.44)
TST + Stand Init	2.61 (0.13)	0.87 (0.29)	8.68 (0.01)	0.65 (0.19)	9.53 (0.01)	9.88 (0.00)
TST + Adv Regen + Mature + Stand Init	5.72 (0.03)	1.37 (0.22)	10.64 (0.00)	2.16 (0.09)	**0.00 (0.99)**	**0.00 (0.55)**
Best model Pearson's *r* validation	0.99	0.99	0.95	0.97	0.97	0.99

We evaluated model support using AIC_c and selected the top model when several models received similar support (i.e., $\Delta AIC_c < 2$). We then calculated standardized regression coefficients (by standardizing explanatory variables: $(x_i - \bar{x})/SD$) and evaluated the strength of relationships ($\alpha \leq 0.10$). In addition, we evaluated the fit of our top models by assessing hanging rootograms (Kleiber and Zeileis, 2016), which characterize a model's tendencies to over- or under-predict across the gradient of the response variable (intensity of patch use in our case). As a final measure of model fit, we also computed the Pearson's correlation coefficient between observed and expected counts > 0; we used values > 0 because hurdle models (by design) predict exactly the number of zeros observed within the fitted dataset (Kleiber and Zeileis, 2016). Lastly, we evaluated if there was evidence of spatial autocorrelation in the residuals from our top models using Moran's *I* (Moran, 1950) correlograms across 20 lag distances. Moran's *I* ranges between -1 and 1, which indicates perfect dispersion and perfect correlation, respectively. Positive autocorrelation in the residuals would indicate our models did not capture an important environmental gradient. We conducted all analyses in program R (R Core Team, 2017) and used the 'countreg' (Kleiber and Zeileis, 2016), 'pscl' (Zeileis et al., 2008), and 'pgirmess' (Giraudoux, 2017) packages.

3. Results

Our initial assessment indicated that the intensity of use by Canada lynx was distributed similarly across seasons (winter and summer) and that there was little use by lynx up to ~10 years after a silvicultural treatment regardless of type (Fig. 4a). Our ANOVA indicated differences in time since treatment for patches occupied by lynx across regeneration cuts, selection cuts, and thinnings (winter: $F_{2,1030} = 161.59$, $p < 0.001$, $R^2 = 0.24$; summer: $F_{2,1231} = 176.54$, $p < 0.001$, $R^2 = 0.22$). On average, Canada lynx used thinning treatments 14–20 years faster (winter: $\bar{x} = 20$ years since treatment, 95% CI = 19–21 years since treatment; summer: $\bar{x} = 20$ since treatment, 95% CI = 19–21 years since treatment) than regeneration cuts (winter: $\bar{x} = 34$ years since treatment, 95% CI = 33–35 years since treatment; summer: $\bar{x} = 34$ years since treatment, 95% CI = 33–34 years since treatment) or selection cuts (winter: $\bar{x} = 39$ years since treatment, 95% CI = 38–41 years since treatment; summer: $\bar{x} = 41$ years since treatment, 95% CI = 40–42 years since treatment; Fig. 4b). Although we observed statistical differences among all treatments, the largest effect was associated with thinnings relative to regeneration and selection cuts (Fig. 4b). Consistent with these statistical differences, cumulative use (in both winter and summer) by Canada lynx reached 50% (i.e., half) at ~20 years after a thinning treatment (Fig. 4c), whereas it took ~34–40 years after a selection or regeneration cut to reach 50% use. The cumulative proportion of use by lynx was distributed similarly for regeneration and selection cuts (Fig. 4c) despite the differing levels of vegetation impact associated with tree harvest as measured by the NBR (Fig. 2b). Overall, these univariate assessments indicated that Canada lynx exhibit temporal differences in their use across silvicultural treatments (i.e., thinning versus regeneration or selection cuts).

Results from our multivariate hurdle models provided additional detail concerning how Canada lynx used differing silvicultural treatments over time (Table 2). Lynx use of regeneration cuts in the winter ($n = 1,378$) was best explained by only time since treatment; no other models were supported (i.e., < 2 ΔAIC_c). The effect of time since treatment was statistically positive, which indicated that both the probability of occupancy and the intensity of lynx use increased with time since treatment (Table 3). In the summer ($n = 1,405$), lynx use of regeneration cuts was best characterized by time since treatment, the proportion of advanced regeneration in the neighborhood, and their interaction (Table 2; although, there was some evidence stand initiation positively influenced patch occupancy by lynx). The only statistical effect from our top model was the interaction between time since treatment and advanced regeneration for the intensity of lynx use (Fig. 5a, Table 3), which indicated that lynx use was relatively static with a low amount of advanced regeneration in the neighborhood, but increased with time when advanced regeneration was abundant in the neighborhood (Fig. 5a). This pattern suggested that abundant advanced regeneration had a negative effect on lynx use early (e.g., 0–30 years after treatment), but facilitated more use of regeneration cuts later in time (e.g., > 40 years after treatment); that is, a spatio-temporal functional response in patch use by Canada lynx. Collectively, these results indicated that (1) time since treatment was important for lynx use of harsh regeneration cuts (particularly in the winter), and (2) the structural composition in the neighborhood surrounding a treated patch influenced lynx use over time.

Similar to regeneration cuts, our top models characterizing lynx use of selection cuts varied by season (Table 2). During winter ($n = 223$), patch use was best explained by time since treatment, the proportion of mature forest within the neighborhood, and their interaction (Table 3). However, the interaction was only significant for intensity of lynx use and indicated that the effect of time since treatment depended on the amount of mature forest in the neighborhood (Fig. 5b). When mature forest was abundant, lynx were less inclined to use the selection cut over time; however, when mature forest was low, lynx increasingly used the selection cut after ~40 years (Fig. 5b). This was consistent with lynx preferentially using mature forest over selection cuts when the former was abundant in the neighborhood of a treated patch. In the summer ($n = 221$), our top model included time since treatment and the proportion of advanced regeneration in the neighborhood (Table 2;

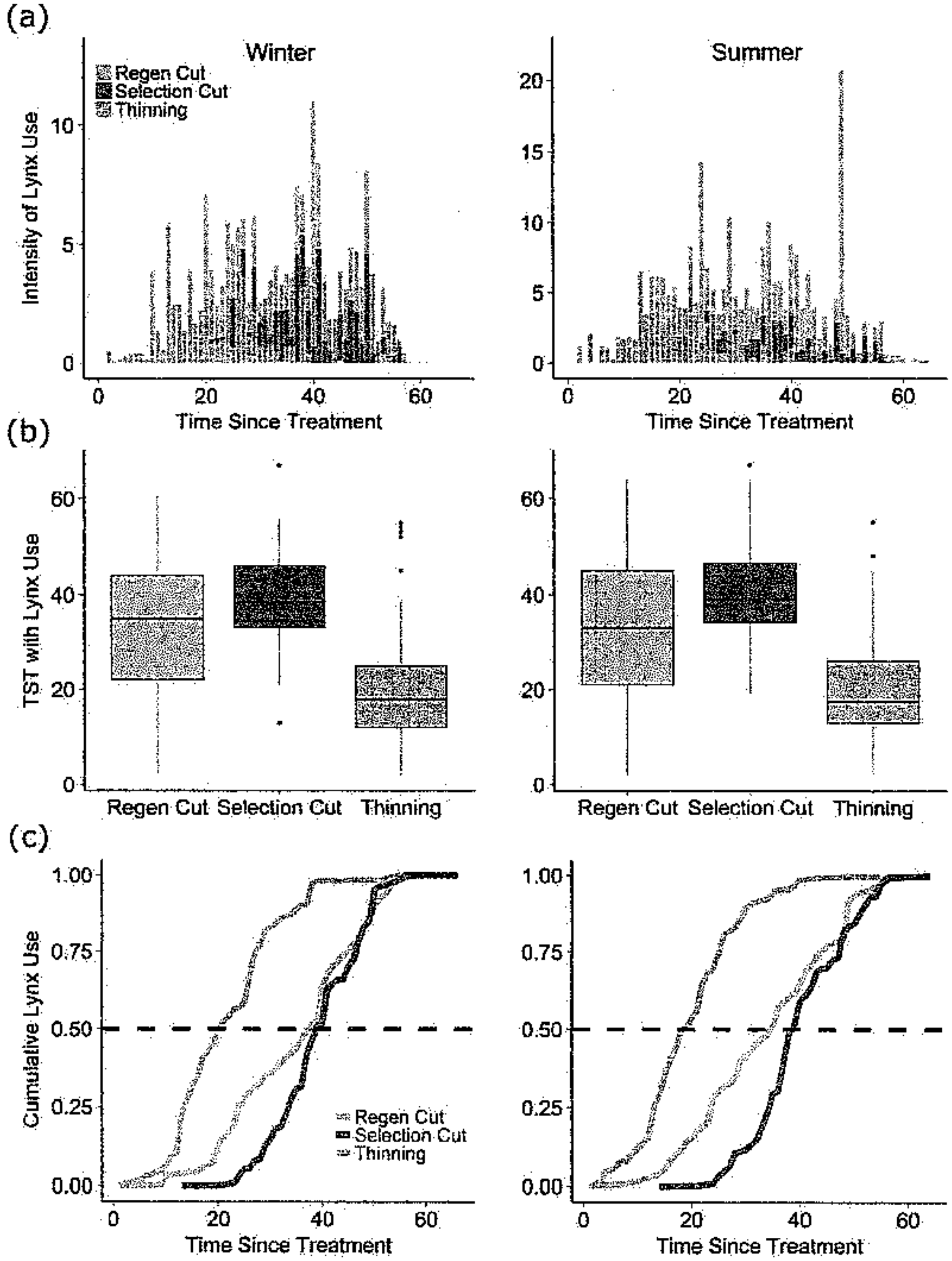

Fig. 4. Temporal distribution of habitat use by Canada lynx (*Lynx canadensis*) associated with different silvicultural treatments. (a) Standardized intensity of patch use by treatment and across a gradient in time since treatment (TST; 1–67 years post-treatment). (b) Boxplots of TST by strata for all patches that were used by lynx (i.e., ≥1 lynx location). (c) Cumulative intensity of lynx use by treatment and across a gradient in TST (1–67 years post-treatment). The dashed lines in (c) indicate 50% of the cumulative use, which is approximately equal to the median value in (b). Regen indicates regeneration.

although, there was evidence that the intensity of lynx use was positively related to stand initiation). However, the only statistical effects were associated with the intensity of lynx use (Tables 2 and 3). The intensity of lynx use was positively related to both time since treatment and advanced regeneration in the neighborhood. These results further emphasized that (1) time since treatment was important for lynx use of harsher treatments (e.g., selection cuts), and (2) the structural composition in the neighborhood surrounding a treated patch influenced lynx use.

Finally, use of thinning treatments by Canada lynx was generally driven by the same factors during winter ($n = 416$) and summer ($n = 422$). Lynx use was influenced by the proportion of stand initiation, advanced regeneration, and mature forest in the neighborhood, but the effect of time since treatment was only significant during the winter (Table 2). The standardized regression coefficients characterizing lynx use of thinning treatments indicated that (1) the surrounding neighborhood was more important than time since treatment, and (2) that the neighborhood effects varied in direction and magnitude across

Table 3

Standardized regression coefficients for covariates within the selected hurdle models characterizing how silvicultural treatment influenced patch occupancy and intensity of use by Canada lynx (*Lynx canadensis*). Coefficients are shown for both the binomial and negative binomial regressions, characterizing occupancy and intensity of use, respectively. Bold indicates support for a spatio-temporal functional response in patch use by lynx. TST indicates time since treatment, Adv Regen indicates advanced regeneration, and Stand Init indicates stand initiation.

Covariate	Regeneration cut		Selection cut		Thinning	
	Winter	Summer	Winter	Summer	Winter	Summer
TST						
Occupancy	0.442***	0.051	0.381**	0.138	0.054	−0.040
Intensity of use	0.614***	0.079	0.298**	0.267**	0.158	-0.096
Mature						
Occupancy	–	–	−0.346$^{\gamma*}$	–	−0.335$^{\gamma**}$	0.267$^{\gamma*}$
Intensity of use	–	–	−0.314$^{\gamma***}$	–	0.256$^{\gamma**}$	-0.161$^{\gamma*}$
Adv regen						
Occupancy	–	−0.093$^{\gamma}$	–	0.002†	−0.207$^{\gamma}$	0.570†**
Intensity of use	–	−0.064$^{\gamma}$	–	0.221$^{\gamma**}$	−0.029$^{\gamma}$	-0.133†*
Stand Init						
Occupancy	–	–	–	–	−0.285$^{\gamma**}$	0.095$^{\gamma}$
Intensity of use	–	–	–	–	0.389$^{\gamma***}$	0.194$^{\gamma**}$
TST mature						
Occupancy	–	–	−0.126	–	–	–
Intensity of use	–	–	−0.409***	–	–	–
TST Adv Regen						
Occupancy	–	0.057		–	–	–
Intensity of use	–	0.145***		–	–	–

† 1.5 km neighborhood.

$^{\gamma}$ 4 km neighborhood.

* $\alpha < 0.10$.

** $\alpha < 0.05$.

*** $\alpha < 0.01$.

seasons and lynx responses (i.e., occupancy and intensity of use; Table 3). The probability of lynx occupancy during winter was negatively related to the amount of stand initiation and mature forest in the neighborhood, whereas the intensity of lynx use was positively related to these two variables (Table 3). During summer, lynx occupancy was positively related to the amount of advanced regeneration and mature forest in the neighborhood, but contrastingly the intensity of lynx use was negatively related to these factors (Table 3). The intensity of lynx use was also positively related to the amount of stand initiation in the neighborhood (Table 3). In contrast to regeneration and selection cuts, the forest structure surrounding a thinning treatment was consistently more important for lynx use than the effect of time since treatment.

All model evaluations provided evidence of appropriate model fit. The correlations between observed and expected counts > 0 were consistently high, which suggested strong model performance (Table 2; $r \geq 0.95$). In addition, we observed no consistent spatial autocorrelation in the residuals (all Moran's I values ≤ 0.10) across all lag distances.

4. Discussion

Relatively few studies have evaluated the effect of different silvicultural actions on the resource use of forest carnivores (e.g., Cushman et al., 2011; Tigner et al., 2015; Scrafford et al., 2017), despite the management controversy associated with manipulating forests occupied by these sensitive species (e.g., Howard, 2016). To our knowledge, our work is the first to assess the effect of silvicultural actions on Canada lynx. Importantly, we discovered that lynx use silvicultural treatments. However, use of any treatment (i.e., regeneration cut, selection cut, or thinning) was low up to ~10 years post-treatment. This suggests there is a cost regardless of treatment type, which is consistent with previous work highlighting a ~10 year negative impact of precommercial thinning on snowshoe hare densities (Homyack et al., 2007). The alignment of these ~10 year responses for lynx and snowshoe hares is consistent with ecological predictions because Canada lynx rely heavily on snowshoe hares as a prey resource (e.g., Mowat et al., 1996; Squires and Ruggiero, 2007; Ivan and Shenk, 2016). In addition, we found that Canada lynx use thinning treatments at a faster rate over time than either selection or regeneration harvests (Fig. 4). Contrary to our expectations, lynx used selection and regeneration cuts similarly over time despite the differences we observed in vegetation impact as measured via NBR (Fig. 2). Moreover, the composition and abundance of forest structural stages surrounding a particular treatment (e.g., Fig. 3) influences how lynx use that treatment. In some cases, both the probability of occupancy and the intensity of patch use by Canada lynx was influenced by the surrounding forest structure, which exemplified a spatial functional response in habitat use (*sensu* Mysterud and Ims, 1998). This was similar to previous work demonstrating the importance of the surrounding landscape for the patch use of woodland caribou (Lesmerises et al., 2013) and pygmy rabbits (*Brachylagus idahoensis*; McMahon et al., 2017). However, patch use by Canada lynx was also characterized by an interaction between time since treatment and the composition of forest structure in the neighborhood, which indicated a spatio-temporal functional response (Fig. 5). In other words, vegetation recovery after a silvicultural treatment and the existing forest structure surrounding a treatment interactively influenced the behavior of Canada lynx. Collectively, this work fills an important knowledge gap in Canada lynx spatial ecology. Forest managers can apply our spatio-temporal understandings to develop refined strategies aimed at both forest management and lynx habitat conservation.

The relationship between time since treatment and patch use by Canada lynx was generally similar across our univariate and regression analyses. For instance, our univariate assessments indicated lynx use thinnings sooner after a harvest than selection or regeneration cuts (Fig. 4), which aligned with our index of treatment severity based on the NBR (Fig. 2). Our regression analyses indicated that the effect of time since treatment was always positive for lynx use, but the effect was

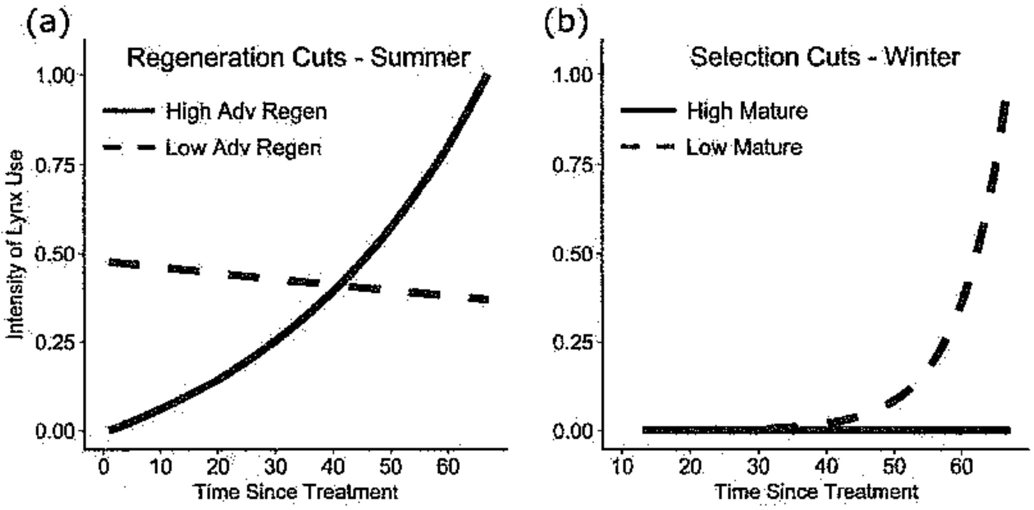

Fig. 5. Spatio-temporal interactions (i.e., a spatio-temporal functional response) predicted from our selected hurdle models characterizing the intensity of Canada lynx (*Lynx canadensis*) use (scaled between 0 and 1) for regeneration and selection cuts. In other words, the intensity of lynx use within a patch depends on the amount of advanced regeneration or mature forest in the 4 km and 1.5 km neighborhood (respectively) surrounding the patch as well as the time since treatment. Predicted intensity of use was generated from the negative binomial regression within the hurdle model. (a) Indicates the predicted intensity of lynx use during summer for patches that received a regeneration cut. (b) Indicates predicted intensity of lynx use during winter for patches that received a selection cut. The proportion for 'High Adv Regen' was 0.30 and 'Low Adv Regen' was 0.10, while the proportion for 'High Mature' was 0.80 and 'Low Mature' was 0.30. Adv Regen indicates advanced regeneration.

stronger for regeneration cuts followed by selection cuts and thinnings, respectively (Tables 2 and 3; again, aligning with treatment severity). Finally, as predicted, time since harvest generally exhibited a stronger effect on lynx use during the winter as compared to the summer (Table 3), but this was only apparent in our regression analyses.

These temporal patterns were consistent with habitat selection by Canada lynx in the Rocky Mountains, U.S. For example, Canada lynx exhibit strong multi-scale selection for advanced regeneration and mature forest likely because of abundant and accessible snowshoe hares (Squires et al., 2010; Ivan et al., 2014; Ivan and Shenk, 2016; Holbrook et al., 2017b). In our study area, the stage of advanced regeneration takes at least ~25 years to develop (Holbrook et al., 2017a), which aligns with the initial use of regeneration and selection cuts by lynx (Fig. 4a and 4c). Further, Canada lynx increasingly use mature structural stages during the winter months (Squires et al., 2010; Holbrook et al., 2017a), suggesting more time might be needed to develop winter habitat as compared to summer habitat. Heterogeneous disturbances such as thinnings, however, seemingly facilitate the development of advanced regeneration and mature forests at a faster rate than selection or regeneration harvests given the earlier use by lynx (Fig. 4c). These results have implications concerning the temporal dimensions of forest treatments aimed at improving Canada lynx habitat.

Furthermore, lynx exhibited different responses to the composition of forest structural stages in the neighborhood surrounding thinnings based on the hierarchical level of behavior; that is, the probability of lynx occupancy (first level) and the intensity of lynx use (second level). Many studies have demonstrated the hierarchical habitat relationships (e.g., Johnson, 1980; Rettie and Messier, 2000; DeCesare et al., 2012; Holbrook et al., 2017a; McMahon et al., 2017), and our insights build on this work. For instance, increasing stand initiation in the neighborhood negatively influenced lynx occupancy of thinnings during the winter. This is likely because Canada lynx strongly avoid stand initiation (Holbrook et al., 2017a), and particularly so in the winter, thus decreasing the probability of patch use when stand initiation is abundant in the surrounding area. In contrast, stand initiation positively influenced the intensity of lynx use within a thinned patch during the winter and summer. This was conceivable because once a lynx occupies a thinning, they might then chose to remain within the patch versus moving out into an avoided structural stage (i.e., stand initiation). Other studies using analytical procedures similar to ours have demonstrated differential responses depending on the hierarchical level of the response (e.g., occupancy or intensity of use) for woodland caribou and pygmy rabbits (Lesmerises et al., 2013; McMahon et al., 2017).

We also observed situations where the effect of forest structure in the surrounding neighborhood was similar across the hierarchical levels of behavior. For example, Canada lynx exhibited a reduced probability of occupancy and intensity of use for treated patches when the neighborhood contained abundant mature forest (Table 3). In fact, when mature forest was abundant in the neighborhood of selection cuts, the intensity of use by Canada lynx remained low regardless of time since treatment (Fig. 5b). The negative influence of mature forest on lynx resource use was likely associated with the benefits provided by mature forests resulting in lynx selecting this stage and avoiding the treated patches nearby. A similar mechanism was suggested to explain the fast and direct movement of Pacific marten through resource-poor stands (i.e., open areas) versus the slow, more deliberate movements in resource-rich stands (Moriarty et al., 2016). Mature forests provide abundant, temporally stable, and accessible snowshoe hares within the Rocky Mountains (Griffin and Mills, 2009; Ivan et al., 2014; Ivan and Shenk, 2016; Holbrook et al., 2017b), and therefore lynx spend a substantial amount of time within this structural stage (Squires et al., 2010; Holbrook et al., 2017a).

Our suite of insights concerning the spatio-temporal responses of Canada lynx to silvicultural actions were in part a result of our novel approach to stratifying silvicultural treatments. We retroactively evaluated vegetation responses over time using the NBR, which ensured our treatment stratification was ecologically relevant. We then demonstrated that this approach related to Canada lynx, with lynx using a high value and narrow range of NBR (Fig. 2). Future work examining animal responses to forest manipulations could apply our approach to characterize ecologically distinct treatments through time. This is an important contribution because often it is assumed that different database labels, such as classifications of silvicultural actions (e.g., with the FACTS database), represent ecological differences, which we demonstrated to be a false assumption (e.g., Fig. 2a).

5. Conclusion

A difficult challenge within publically managed forests lies at the intersection of silvicultural actions and the management of forest-dwelling species that are of conservation concern (e.g., Stephens et al., 2014; Howard, 2016). To assist in narrowing the gap between silviculture and species conservation, we evaluated how forest treatments influence resource use of Canada lynx, a threatened carnivore in the contiguous U.S. (USFWS, 2000). First, we demonstrated that lynx clearly use silviculture treatments, but there is a ~10 year cost of implementing any treatment (thinning, selection cut, or regeneration cut) in terms of resource use by Canada lynx. This temporal cost is associated with lynx preferring advanced regenerating and mature structural stages (Squires et al., 2010; Holbrook et al., 2017a) and is consistent with previous work demonstrating a negative effect of precommerical thinning on snowshoe hare densities for ~10 years (Homyack et al., 2007). Second, if a treatment is implemented, Canada lynx used thinnings at a faster rate post-treatment (e.g., ~20 years post-treatment to reach 50% lynx use) than either selection or regeneration cuts (e.g., ~34–40 years post-treatment to reach 50% lynx use). Lynx appear to use regeneration and selection cuts similarly over time suggesting the difference in vegetation impact between these treatments made little difference concerning the potential impacts to lynx (Fig. 4c). Third, Canada lynx tend to avoid silvicultural treatments when a preferred structural stage (e.g., mature, multi-storied forest or advanced regeneration) is abundant in the surrounding landscape, which highlights the importance of considering landscape-level composition as well as recovery time. For instance, in an area with low amounts of mature forest in the neighborhood, lynx use of recovering silvicultural treatments would be higher versus treatments surrounded by an abundance of mature forest (e.g., Fig. 3b). This scenario captures the importance of post-treatment recovery for Canada lynx when the landscape context is generally composed of lower quality habitat. Overall, these three items emphasize that both the spatial arrangement and composition as well as recovery time are central to balancing silvicultural actions and Canada lynx conservation. Our work here represents an important step in filling knowledge gaps at the intersection of disciplines, such as silviculture and animal ecology, which is essential for the future development of pragmatic solutions.

Acknowledgements

We acknowledge the U.S. Department of Agriculture, U.S. Forest Service Region 1 (award number: 12-CS-11221635-176), and the U.S. Forest Service National Carnivore program for their support of this work. We especially thank the Seeley Lake District, Lolo National Forest, for their continued logistical support for over a decade that facilitated our research. In addition, we thank countless field technicians for diligently collecting data under difficult conditions. Finally, we acknowledge S. Fox and two anonymous reviewers for providing thoughtful feedback that improved our manuscript.

Appendix A.

Silvicultural treatment stratification from the U.S. Forest Service's FACTS database.

Table A.1
Reclassification table showing the raw classification from the U.S. Forest Service's FACTS database to our first and final set of silvicultural treatments.

FACTS labels	First set of potential treatments	Final set of treatments
Group selection cut	Group selection cut	Selection cut
Single-tree selection cut	Group selection cut	Selection cut
Liberation cut	Liberation cut	Selection cut
Shelterwood preparatory cut	Improvement cut	Thinning
Improvement cut	Improvement cut	Thinning
Seed-tree preparatory cut	Improvement cut	Thinning
Commercial thin	Improvement cut	Thinning
Stand clearcut	Regen cut	Regen cut
Patch clearcut (w/leave trees)	Regen cut	Regen cut
Stand clearcut (w/leave trees)	Regen cut	Regen cut
Patch clearcut	Regen cut	Regen cut
Seed-tree final cut	Regen cut	Regen cut
Seed-tree seed cut (with and without leave trees)	Regen cut	Regen cut
Shelterwood establishment cut (with or without leave trees)	Regen cut	Regen cut
Two-aged seed-tree seed and removal Cut (w/res)	Regen cut	Regen cut
Two-aged shelterwood establishment and removal Cut (w/ res)	Regen cut	Regen cut
Two-aged shelterwood establishment Cut (w/res)	Regen cut	Regen cut
Certification of natural regeneration with site prep	Natural regen	NA
Certification of natural regeneration without site prep	Natural regen	NA
Initiate natural regeneration	Natural regen	NA
Fill-in or Replant Trees	Planted	NA
Plant Trees	Planted	NA
Planting propagules and cuttings	Planted	NA
Wildlife habitat seeding and planting	Planted	NA
Precommercial thin	Precommercial thin	Thinning

References

Abele, S.L., Wirsing, A.J., Murray, D.L., 2013. Precommercial forest thinning alters abundance but not survival of snowshoe hares. J. Wildl. Manage. 77, 84–92.

Bentz, B.J., Régnière, J., Fettig, C.J., Hansen, E.M., Hayes, J.L., Hicke, J.A., Kelsey, R.G., Negrón, J.F., Seybold, S.J., 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. Bioscience 60, 602–613.

Beyer, H. 2012. Geospatial Modelling Environment. Version 0.7.3.0. < http://www.spatialecology.com/gme > .

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer, New York, New York, USA.

Cushman, S.A., Raphael, M.G., Ruggiero, L.F., Shirk, A.S., Wasserman, T.N., O'Doherty, E., 2011. Limiting factors and landscape connectivity: the American marten in the Rocky Mountains. Landscape Ecol. 26, 1137–1149.

DeCesare, N.J., Hebblewhite, M., Schmiegelow, F., Hervieux, D., McDermid, G.J., Neufeld, L., Bradley, M., Whittington, J., Smith, K.G., Morgantini, L.E., Wheatley, M., Musiani, M., 2012. Transcending scale dependence in identifying habitat with resource selection functions. Ecol. Appl. 22, 1068–1083.

Escuin, S., Navarro, R., Fernández, P., 2008. Fire severity assessment by using NBR (Normalized Burn Ratio) and NDVI (normalized difference vegetation index) derived from LANDSAT TM/ETM images. Int. J. Remote Sens. 29, 1053–1073.

ESRI (Environmental Systems Research Institute), 2011. ArcGIS Desktop: Release 10. Redlands, California.

Fuller, A.K., Harrison, D.J., Vashon, J.H., 2007. Winter habitat selection by Canada lynx in Maine: prey abundance or accessibility? J. Wildl. Manage. 71, 1980–1986.

Giraudoux, P. 2017. Pgirmess: Data Analysis in Ecology. R Package Version 1.6.7. < https://CRAN.R-project.org/package=pgirmess > .

Griffin, P.C., Mills, L.S., 2007. Precommercial thinning reduces snowshoe hare abundance in the short term. J. Wildl. Manage. 71, 559–564.

Griffin, P.C., Mills, L.S., 2009. Sinks without borders: snowshoe hare dynamics in a complex landscape. Oikos 118, 1487–1498.

Harris, S., Veraverbeke, S., Hook, S., 2011. Evaluating spectral indices for assessing fire severity in chaparral ecosystems (southern California) using MODIS/ASTER (MASTER) airborne simulator data. Remote Sensing 3, 2403–2419.

Holbrook, J.D., Squires, J.R., Olson, L.E., DeCesare, N.J., Lawrence, R.L., 2017a. Understanding and predicting habitat for wildlife conservation: the case of Canada lynx at the range periphery. Ecosphere 8, e01939.

Holbrook, J.D., Squires, J.S., Olson, L.E., Lawrence, R.L., Savage, S., 2017b. Multi-scale habitat relationships of snowshoe hares (*Lepus americanus*) in the mixed conifer landscape of the Northern Rockies, USA: cross-scale effects of horizontal cover with implications for forest management. Ecol. Evol. 7, 125–144.

Homyack, J.A., Harrison, D.J., Krohn, W.B., 2007. Effects of precommercial thinning on snowshoe hares in Maine. J. Wildl. Manage. 71, 4–13.

Howard, K., 2016. Petition of The Day, SCOTUSblog. July 20, 2016 < http://www.scotusblog.com/2016/07/petition-of-the-day-963/ > .

Ivan, J.S., White, G.C., Shenk, T.M., 2014. Density and demography of snowshoe hares in central Colorado. J. Wildl. Manage. 78, 580–594.

Ivan, J.S., Shenk, T.M., 2016. Winter diet and hunting success of Canada lynx in Colorado. J. Wildl. Manage. 80, 1049–1058.

Jones, G.M., Gutiérrez, R.J., Tempel, D.J., Whitmore, S.A., Berigan, W.J., Peery, M.Z., 2016. Megafires: an emerging threat to old-forest species. Front. Ecol. Environ. 14, 300–306.

Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61, 65–71.

Kleiber, C., Zeileis, A., 2016. Visualizing count data regressions using rootograms. Am. Statis. 70, 296–303.

Koehler, G.M., Maletzke, B.T., Von Kienast, J.A., Aubry, K.B., Wielgus, R.B., Naney, R.H., 2008. Habitat fragmentation and the persistence of lynx populations in Washington state. J. Wildl. Manage. 72, 1518–1524.

Lesmerises, F., Ouellet, J.P., Dussault, C., St-Laurent, M.H., 2013. The influence of landscape matrix on isolated patch use by wide-ranging animals: conservation lessons for woodland caribou. Ecol. Evol. 3, 2880–2891.

Maletzke, B.T., Koehler, G.M., Wielgus, R.B., Aubry, K.B., Evans, M.A., 2008. Habitat conditions associated with lynx hunting behavior during winter in northern Washington. J. Wildl. Manage. 72, 1473–1478.

Montgomery, R.A., Roloff, G.J., Millspaugh, J.J., Nylen-Nemetchek, M., 2014. Living amidst a sea of agriculture: predicting the occurrence of Canada lynx within an ecological island. Wildlife Biology 20, 145–154.

Moran, P.A., 1950. Notes on continuous stochastic phenomena. Biometrika 37, 17–23.

Moriarty, K.M., Epps, C.E., Zielinski, W.J., 2016. Forest thinning changes movement patterns and habitat use by Pacific marten. J. Wildl. Manage. 80, 621–633.

McCann, N.P., Moen, R.A., 2011. Mapping potential core areas for lynx (*Lynx canadensis*) using pellet counts from snowshoe hares (*Lepus americanus*) and satellite imagery. Can. J. Zool. 89, 509–516.

McMahon, L.A., Rachlow, J.L., Shipley, L.A., Forbey, J.S., Johnson, T.R., 2017. Habitat selection differs across hierarchical behaviors: selection of patches and intensity of patch use. Ecosphere 8, e01993.

Mowat, G., Slough, B.G., Boutin, S., 1996. Lynx recruitment during a snowshoe hare population peak and decline in southwest Yukon. J. Wildl. Manage. 60, 441–452.

Mullahy, J., 1986. Specification and testing of some modified count data models. Journal of Econometrics 33, 341–365.

Mysterud, A., Ims, R.A., 1998. Functional responses in habitat use: availability influences relative use in trade-off situations. Ecology 79, 1435–1441.

Poole, K.G., Wakelyn, L.A., Nicklen, P.N., 1996. Habitat selection by lynx in the Northwest Territories. Can. J. Zool. 74, 845–850.

R Core Team, 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. < https://R-project.org/ > .

Rettie, W.J., Messier, F., 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography 23, 466–478.

Savage, S., Lawrence, R., Squires, J., Holbrook, J., Olson, L., Braaten, J., Cohen, W., 2018. Shifts in forest structure in northwest Montana from 1972 to 2015 using the Landsat archive from multispectral scanner to operational land imager. Forests 9, 157.

Scrafford, M.A., Avgar, T., Abercrombie, B., Tigner, J., Boyce, M.S., 2017. Wolverine habitat selection in response to anthropogenic disturbance in the western Canadian boreal forest. For. Ecol. Manage. 395, 27–36.

Simons-Legaard, E.M., Harrison, D.J., Krohn, W.B., Vashon, J.H., 2013. Canada lynx occurrence and forest management in the Acadian Forest. J. Wildl. Manage. 77, 567–578.

Squires, J.R., Ruggiero, L.F., 2007. Winter prey selection of Canada lynx in northwestern Montana. J. Wildl. Manage. 71, 310–315.

Squires, J.R., Decesare, N.J., Kolbe, J.A., Ruggiero, L.F., 2010. Seasonal resource selection of Canada lynx in managed forests of the northern Rocky Mountains. J. Wildl. Manage. 74, 1648–1660.

Squires, J.R., DeCesare, N.J., Olson, L.E., Kolbe, J.A., Hebblewhite, M., Parks, S.A., 2013. Combining resource selection and movement behavior to predict corridors for Canada lynx at their southern range periphery. Biol. Conserv. 157, 187–195.

Stephens, S.L., Bigelow, S.W., Burnett, R.D., Collins, B.M., Gallagher, C.V., Keane, J., Kelt, D.A., North, M.P., Roberts, L.J., Stine, P.A., Van Vuren, D.H., 2014. California spotted owl, songbird, and small mammal responses to landscape fuel treatments. Bioscience 64, 893–906.

Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., Ransome, D.B., 2013. Stand structure and small mammals in intensively managed forests: scale, time, and testing extremes. For. Ecol. Manage. 310, 1071–1087.

Sweitzer, R.A., Furnas, B.J., Barrett, R.H., Purcell, K.L., Thompson, C.M., 2016. Landscape fuel reduction, forest fire, and biophysical linkages to local habitat use and local persistence of fishers (*Pekania pennanti*) in Sierra Nevada mixed-conifer forests. For. Ecol. Manage. 361, 208–225.

Tempel, D.J., Gutiérrez, R.J., Whitmore, S.A., Reetz, M.J., Stoelting, R.E., Berigan, W.J., Seamans, M.E., Peery, M.Z., 2014. Effects of forest management on California spotted owls: implications for reducing wildfire risk in fire-prone forests. Ecol. Appl. 24, 2089–2106.

Tigner, J., Bayne, E.M., Boutin, S., 2015. American marten respond to seismic lines in northern Canada at two spatial scales. PLoS One 10, e0118720.

USFWS (United States Fish and Wildlife Service), 2000. Determination of threatened status for the contiguous US distinct population segment of the Canada lynx and related rule: final rule. US Federal Register 65, 16052–16086.

Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase western U.S. forest wildfire activity. Science 313, 940–943.

Zeileis, A., Kleiber, C., Jackman, S., 2008. Regression models for count data in R. J. Stat. Softw. 27 (8), 1–25.

Zielinski, W.J., Thompson, C.M., Purcell, K.L., Garner, J.D., 2013. An assessment of fisher (*Pekania pennanti*) tolerance to forest management intensity on the landscape. For. Ecol. Manage. 310, 821–826.