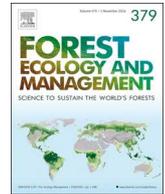




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Management of forests and forest carnivores: Relating landscape mosaics to habitat quality of Canada lynx at their range periphery



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ABSTRACT

Connecting forest management with the conservation of forest-associated animals requires an understanding of habitat quality, as well as identifying long-term silvicultural strategies that align with high quality habitat. It is, therefore, essential to characterize the spatio-temporal dimensions of habitat quality. Here, we leveraged multiple datasets to assess high quality habitat for female Canada lynx (*Lynx canadensis*), a federally threatened forest carnivore in the contiguous U.S. Our datasets included a spatially extensive sample of snowshoe hares (*Lepus americanus*) collected in 2013 ($n = 1340$ plots), an expansive time-series (i.e., 1972–2013) of forest structural classes derived from remote sensing, and a longitudinal dataset where we monitored habitat use and the reproductive success (i.e., litter of kittens present or absent) of female Canada lynx during 1999–2013 ($n = 32$ female lynx over 92 lynx years). Our results indicated that the probability of a female producing kittens was most associated with the connectivity of mature, multistoried forests (composed of mostly spruce-fir). However, the variation among female lynx accounted for $\approx 62\%$ of the total variation explained in litter production, suggesting substantial individual-level variation. Thus, managers can contribute to increased reproductive success of female Canada lynx by facilitating the development of mature forests, but measuring that success will be difficult given the individual variation. In core areas of high quality females (i.e., produced kittens frequently), mature forest was 17% more abundant (i.e., $\approx 60\%$ of the total core area), more connected, less clumpy, and exhibited 2.25-times larger patch sizes than the core areas of low quality females. At the home-range extent, patterns were less pronounced while the abundance of mature forests remained high ($\approx 50\%$) for high quality females. Additionally, we demonstrated that the relative density of snowshoe hares was ≥ 2.8 times higher in advanced regenerating forests compared to all other structural classes, including mature forest. Advanced regenerating forests accounted for $\approx 18\text{--}19\%$ of the core area and home range of high quality female lynx. Combined, our results suggest that a high quality mosaic for female Canada lynx contains $\approx 50\text{--}60\%$ mature forest and $\approx 18\text{--}19\%$ advanced regenerating forest. Furthermore, we used Forest Inventory and Analysis data to characterize the approximate age distribution of advanced regeneration and mature forest, which was relevant for rotation schedules of forest silviculture. Results indicated that advanced regeneration was ≈ 20 to 80 years old while mature forest was ≈ 50 to ≥ 200 years old. Our results provide novel insight into how forest management could increase habitat quality for female Canada lynx, and suggest that multiple silvicultural methods (e.g., intermediate treatments, regeneration harvests) could be employed to maintain a forest mosaic that enhances the ability of females to produce kittens. We concluded by providing a framework that integrates our new insights into a management context with the aim of conserving Canada lynx on multiple-use lands.

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1. Introduction

Conservation of forest-associated animals requires an understanding of habitat quality, along with the development of spatio-temporal management strategies that are consistent with high quality habitat. Habitat quality has been characterized in many ways, but now it is generally accepted that quality is most appropriately defined based on measures of individual or population performance (e.g., individual survival or reproduction, population growth; *sensu* Van Horne, 1983). Numerous studies have devoted substantial resources into characterizing habitat quality for sensitive species, including African lions (*Panthera leo*; Mosser et al., 2009), cheetahs (*Acinonyx jubatus*; Broekhuis, 2018), northern spotted owls (*Strix occidentalis caurina*; Franklin et al., 2000; Dugger et al., 2005), wild dogs (*Lycaon pictus*; Davies et al., 2016), and gray wolves (*Canis lupus*; Uboni et al., 2017). Furthermore, the designation of “critical habitat” is required by the U.S. Endangered Species Act (ESA), which further emphasizes the importance of identifying habitat quality. While habitat quality is an important idea in species conservation, managers of wildlife and forests might find it difficult to apply the concept. Providing detailed information regarding the spatio-temporal aspects of habitat quality is valuable to managers for informing strategies aimed at producing and sustaining high quality habitat (e.g., Graham et al., 1994).

In the contiguous U.S., Canada lynx (*Lynx canadensis*) are a threatened forest carnivore under the ESA (USFWS, 2000) and consequently have been associated with numerous challenges concerning forest management on public lands (e.g., Howard, 2016). Much of the controversy surrounding forest management and Canada lynx conservation is concerning habitat requirements, which in turn implicates questions associated with the relationships among forest management, forest structure and arrangement, and lynx habitat quality. Holbrook et al. (2018) recently described spatio-temporal patterns of habitat use by Canada lynx as a function of differing silvicultural treatments, but they did not address how landscape mosaics from forest management influenced habitat quality for Canada lynx. Thus, there remains a substantial need to provide management-relevant information that helps identify and conserve high quality habitat for Canada lynx over the long-term.

Previous work evaluating habitat relationships of Canada lynx indicated that forest structure is an important factor driving space use (e.g., Koehler et al., 2008; Squires et al., 2010; Simons-Legaard et al., 2013; Montgomery et al., 2014; Holbrook et al., 2017a). Forest structure is a strong determinant of the distribution and accessibility of snowshoe hares (*Lepus americanus*), which is the primary prey of Canada lynx (e.g., Elton and Nicholson, 1942; O’Donoghue et al., 1998; Squires and Ruggiero, 2007; Ivan and Shenk, 2016). In general, mosaics of forest structural classes are present in lynx home ranges (Koehler et al., 2008; Squires et al., 2010; McCann and Moen, 2011; Fuller et al., 2007; Montgomery et al., 2014; Holbrook et al., 2017a; Vianbianchi et al., 2017), but to our knowledge only one study has related such structures to Canada lynx habitat quality. Kosterman et al. (2018) suggested that female Canada lynx in the Rocky Mountains exhibit an income breeding strategy and that successful litter production was associated with intermediate amounts of regenerating forest as well as abundant, well-connected mature forest (within female’s core use areas). However, Kosterman et al. (2018) did not characterize (1) the sensitivity of litter production with respect to differing habitat attributes, (2) the number and spatial arrangement of core use areas (i.e., core areas often contain multiple, spatially distinct units), (3) the age distribution and transition time between forest structural classes, or (4) the forest metrics amenable to forest management (e.g., patch size and arrangement, along with vegetation descriptions). The development of long-term strategies aimed at forest management and Canada lynx conservation requires addressing these knowledge gaps.

Our goal was to characterize the spatio-temporal aspects of forest mosaics that are associated with high quality habitat of Canada lynx in

the Northern Rocky Mountains (hereafter, Northern Rockies), U.S. We incorporated multiple datasets and implemented a multi-step analytical process. First, we evaluated the relationship between forest structural classes and the prevalence of snowshoe hares. This assessment provided an important foundation for the remainder of our work in that Canada lynx depend heavily on snowshoe hares for food (e.g., Elton and Nicholson, 1942; O’Donoghue et al., 1998). Second, we characterized the age distribution and transition time between forest structural classes because the temporal dimensions of forest structure is essential for developing rotation schedules in forest management. Third, we extended the analysis of Kosterman et al. (2018) to assess the sensitivity of female litter production to changes in forest structure, which allowed us to identify the attribute that impacts productivity most. Lastly, we identified the number and arrangement of core use units (within core areas) as well as amount and configuration (e.g., patch size, arrangement, shape) of forest structural classes within home ranges of high quality female lynx. This final step was essential to provide the information necessary to integrate our results into forest management. We defined high quality habitat as the forest attributes used by female lynx that consistently produced a litter of kittens. We leveraged many datasets in our analyses, which included a spatially extensive sample of snowshoe hares collected in 2013 (Holbrook et al., 2017b), an expansive time-series (e.g., 1972–2013) of mapped forest structural classes (Savage et al., 2018), and a longitudinal dataset where we monitored habitat use and the reproductive success of female Canada lynx during 1999–2013 (Kosterman et al., 2018).

Based on previous work from the same lynx population (e.g., Squires et al., 2008, 2010, Holbrook et al., 2017a; Kosterman et al., 2018), we developed three expectations. We predicted (1) the reproductive success of female Canada lynx would be most sensitive to changes in mature, multistoried forests, (2) core use areas of high quality females (i.e., those that produce kittens most frequently) would be spatially centralized, and (3) high quality females would inhabit home ranges composed of larger and more connected patches of older forest structures. Snowshoe hares are generally more abundant and accessible (i.e., higher lynx kill rates) in older forest structures in the Rocky Mountains (e.g., Griffin and Mills, 2009; Squires et al., 2010; Berg et al., 2012; Ivan and Shenk, 2016), which was the primary basis of our predictions. Indeed, multiple studies have demonstrated that Canada lynx exhibit higher reproductive success when snowshoe hares are abundant and accessible, as compared to when hares are scarce (e.g., Mowat et al., 1996; Slough and Mowat, 1996). Collectively, our work advances the understanding of Canada lynx habitat quality, but more broadly serves as an example of relating habitat-fitness relationships to on-the-ground management for the shared vision of managing forests and conserving forest carnivores.

2. Materials and methods

2.1. Study area

Our study occurred in the Northern Rockies of northwestern Montana, U.S., within the distribution of Canada lynx (Fig. 1; see Squires et al., 2013 for additional details). This area covers approximately 3.6 million ha and is mostly composed of public lands (about 80%), but with commercial and private forest lands included as well. Across ownerships, there are differing amounts and kinds of human use and timber harvest. However, the majority of the area occupied by Canada lynx and snowshoe hares is within federally managed lands (Holbrook et al., 2017a, 2017b), which includes multiple-uses such as timber harvest.

Our study area supports a diversity of forest structural classes and species compositions across an elevational gradient from ≈ 550 to ≈ 3360 m. These cool mixed-conifer forests contain Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), western larch (*Larix occidentalis*), subalpine fir (*Abies lasiocarpa*), and Engelmann

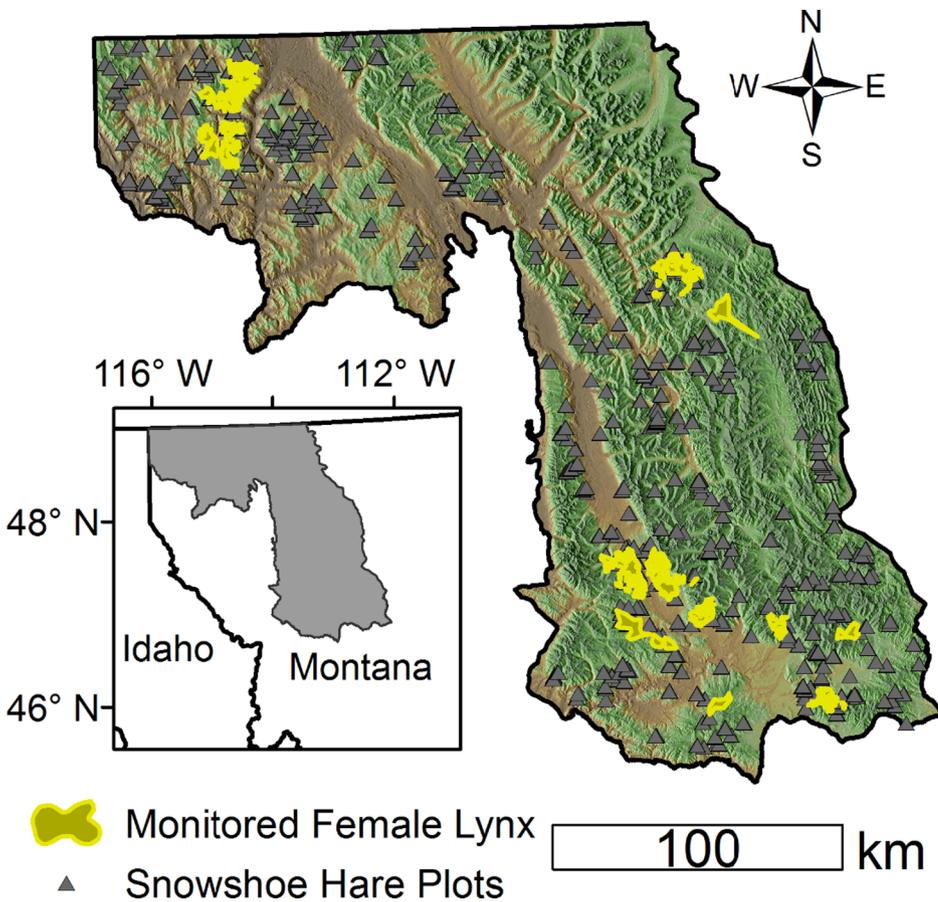


Fig. 1. Study area in northwestern Montana, U.S. where we sampled female Canada lynx (*Lynx canadensis*) and snowshoe hares (*Lepus americanus*) during 1999–2013. We sampled 1340 plots and counted snowshoe hare pellets during 2013 and monitored the reproductive success (i.e., producing a litter of kittens) of 32 females from 1999 to 2013.

spruce (*Picea engelmannii*) trees along with a variety of shrubs, forbs, and grasses. Multiple forest structural classes (e.g., young to old) were well distributed across our study area, to which Canada lynx exhibited strong behavioral responses in terms of habitat use and selection (Holbrook et al., 2017a, 2018). The relatively distinct (albeit coarse) structural classes included: (1) stand initiation (e.g., very few large trees remaining with open canopy), (2) sparse forests (e.g., sparse overstory with low canopy cover, which could be naturally present or mechanically created), (3) advanced regenerating forests (e.g., revegetated stands from past forest harvest with mid-sized trees that provide dense horizontal and canopy cover), and (4) mature forests (e.g., multistoried stands with dense horizontal and vertical cover from older trees that are more complex than advanced regeneration).

The distribution and abundance of these structural classes were spatially predicted on an annual basis by Savage et al. (2018) across the extent of our study area (Fig. 1) over a time-series from 1972 to 2013. Savage et al. (2018) accomplished this by pairing the entire archive of Landsat imagery with field data, and implementing supervised classification techniques along with a series of forest successional rules ensuring a natural progression among structural classes. Mapped structural classes (resolution of 30×30 m pixels) were then validated using confusion matrices ($\approx 80\%$ accuracy) and tree metrics from plot data collected by the USDA Forest Service's Forest Inventory and Analysis (FIA) program, such as tree size and tree density (see Holbrook et al., 2017a; Savage et al., 2018, Appendix A). Additionally, the composition of tree species within each structural class was also evaluated, which suggested a mixed composition, although Engelmann spruce and subalpine fir were consistently more abundant than any other tree species across classes (see Holbrook et al., 2017a).

2.2. Forest structure and snowshoe hares

The distribution and abundance of snowshoe hares were central to our predictions characterizing how forest structural classes influence the reproductive success of female Canada lynx. Previous studies indicated that forest structure influences snowshoe hare occupancy, density, and population dynamics (e.g., Griffin and Mills, 2009; Ivan et al., 2014; Holbrook et al., 2017b). Therefore, we assessed the relationship between snowshoe hares and forest structural class. We expected both occupancy and relative density of snowshoe hares to be highest in the advanced regeneration and mature structural classes and lowest in the sparse and stand initiation classes. We expected this because horizontal cover is presumably higher in advanced regeneration and mature structural classes, and horizontal cover is positively related to snowshoe hare abundance (e.g., Griffin and Mills, 2009; Berg et al., 2012; Ivan et al., 2014; Holbrook et al., 2017b; Gigliotti et al., 2018).

We sampled snowshoe hares using pellet counts at 1340 plots (20×20 m, collected in Holbrook et al., 2017b) randomly distributed across our study area during 2013 (Fig. 1). At each plot, we sampled snowshoe hare presence and relative density by counting (uncleared) pellets within five 5.1×305 cm subplots (Krebs et al., 1987, 2001) placed at plot center and the four edges of a 20×20 m plot. We averaged our counts across the five subplots to develop our metric of snowshoe hare presence (≥ 1 pellet) and relative density (average number of pellets/subplot). Many studies have demonstrated a strong relationship between pellet counts and snowshoe hare densities (e.g., Krebs et al., 1987; Murray et al., 2002; Mills et al., 2005), suggesting pellet counts are an adequate index of relative density. We then intersected each plot with a forest structural class for the year 2013 (Savage

et al., 2018) to identify how occupancy and relative density of hares related to remotely-sensed structural classes. The resulting sample sizes were as follows: 69 plots within the stand initiation class, 348 plots within the sparse class, 206 plots within the advanced regeneration class, and 718 plots within the mature class. We then evaluated differences in the proportion of sites with snowshoe hare pellets as well as average pellet densities (\pm 95% CIs) among these four structural classes.

2.3. Age distribution and transition times of forest structural classes

To inform silvicultural methods and systems designed to conserve Canada lynx over the long-term (e.g., > 50–100 years), we characterized temporal aspects of our forest structural classes (i.e., stand initiation, sparse, advanced regeneration, and mature). For instance, we assessed (1) the distribution of tree ages within our structural stages, and (2) the time required to transition from one structural class to another after a vegetation reset (e.g., after a clearcut). To satisfy our first objective, we intersected our forest structural classes (i.e., mapped in 2013 by Savage et al., 2018) with 550 subplots (\approx 170 m²) collected by the USDA Forest Service's FIA program during 2005–2012. From these plot data, we then examined the distribution of tree ages (i.e., age categories ranging from 0 to \geq 200 years) for each of our forest structural classes, as well as calculated median values (\pm IQR) of tree metrics including basal area weighted DBH, canopy cover, and tree density. We expected the distribution of stand initiation to be the youngest, followed by advanced regeneration and mature forest as the oldest. Sparse was a structural category that could be young or old, and thus we expected a wide age distribution.

To address our second objective, we used the time-series of forest structural classes from Savage et al. (2018) to evaluate how the proportion of structural classes within regeneration cuts (i.e., clearcuts – a complete removal of all conifer trees) changed as a function of time since harvest. We identified 791 regeneration cuts within our study area using the USDA Forest Service's Forest ACTivity Tracking System (FACTS), which is a polygon-based geospatial database of forest management actions. We then calculated the proportion of structural classes (\pm 90% CIs) within each regeneration polygon in each year after harvest (starting at $t + 1$) between 1973 and 2013 (i.e., a 39-year sequence) to characterize how structural classes transitioned across the temporal gradient. We plotted these proportions through time to assess the set of years over which each structural class was dominant. Similar to our previous expectations, we anticipated stand initiation would dominate immediately after a harvest and advanced regeneration and mature forests would take many years to begin establishing. However, in the context of a vegetation reset, we expected sparse forests to act as an intermediary between stand initiation and advanced regeneration coincident with the establishment of taller trees. We used the Geospatial Modelling Environment (Beyer, 2012) and program R (R Core Team, 2017) to complete these analyses.

2.4. Forest mosaics, core use areas, and female quality of Canada lynx

We implemented a two-stage process to characterize the range of values associated with the amount, configuration, and shape of forest structural classes in home ranges of female lynx. First, similar to Kosterman et al. (2018), we developed a model that described the relationship between the proclivity of females to produce a litter of kittens and the composition and arrangement of forest structures. However, extending beyond Kosterman et al. (2018), we evaluated the sensitivity of these relationships and used our model to assign a probability of producing a litter of kittens to each female. Second, we used these predictions to classify each female into a category of low, medium, and high quality based on their tendency to produce litters. We then evaluated core area characteristics (e.g., number of core use units; that is, spatially distinct polygons of the core area) as well as the

amount, configuration, and shape of forest structural classes across the categories of female quality using metrics such as percentage of area, patch size, connectivity, clumpiness, and shape. This second step was essential from a management perspective because silviculturists need detailed information on forest metrics to effectively integrate habitat quality into management actions relevant for Canada lynx.

2.4.1. Step one - models for understanding quality of female lynx

We determined space use and reproductive success (i.e., litter production) for 32 female Canada lynx during 1999–2013 (Fig. 1), which were from the same population presented in Kosterman et al. (2018) but with additional individuals. We captured and handled females using methods approved by the Institutional Animal Care and Use Committee (IACUC permits 4–2008 and TE053737–1) as described in Squires et al. (2008). We collared females with Very High Frequency (VHF) radio-collars (Advanced Telemetry Solutions, Isanti, MN) during 1999–2004 and with store-on-board GPS collars (Lotek Wireless, Newmarket, Ontario, Canada, and Sirtrack Ltd., Havelock North, New Zealand) during 2005–2013. We located females with VHF collars every 1–2 weeks using aerial telemetry, and GPS collars collected a location every 30 min for 24 h every other day. We monitored females until they died, disappeared from the study area, or until the radio-collars failed. We used telemetry to locate and visit natal dens of females within 1–2 weeks of parturition and recorded whether the female produced kittens or not (see Kosterman et al., 2018 for additional details on data collection).

Our analyses required that we estimate the boundary of a female's home range to relate metrics of forest structure to reproductive success. Because of the differences in platforms (some females with VHF and GPS), female lynx received different sampling intensities (range = 20–7238 locations per female). Therefore, we used a non-parametric “adaptive sphere-of-influence” approach to estimate female home ranges; specifically, α -LoCoH, which is a variant of the local convex hull technique (Getz et al., 2007). The LoCoH techniques are more conservative than parametric kernel approaches in estimating home ranges when the number of relocations are low, and they perform better than parametric methods when hard boundaries or non-use holes (e.g., water bodies for terrestrial species) are present within the home range (Getz et al., 2007). We used the α -LoCoH approach ($\alpha = 25$ km, which is the maximum distance between any two locations we observed) to estimate home ranges (i.e., 90% isopleth) and core use areas (i.e., 50% isopleth) for each female Canada lynx. We selected the 90% and 50% isopleth to ensure consistency with Kosterman et al. (2018). We used the *rhr* library (Signer and Balkenhol, 2015) within program R (R Core Team, 2017).

We characterized the amount, configuration, and shape of forest structures experienced by each female lynx at three spatial scales: home ranges, core use areas, and non-core use areas (i.e., home range = core + non-core). For each female, we matched the median year monitored with the coincident year of the predicted forest structural classes from the time-series of Savage et al. (2018). We used FRAGSTATS software (version 4.2; McGarigal et al., 2012) to quantify the landscape metrics that we predicted to describe the prevalence and configuration of forest structural classes for each female Canada lynx.

We calculated four different metrics across our forest structural classes. First, we quantified the percentage of the landscape composed of each class. Second, we calculated the clumpiness index for each forest structural class. Clumpiness (ranges between -1 and 1) represents patch clustering, where a value of -1 indicates maximum disaggregation and 1 indicates maximum aggregation (McGarigal et al., 2012). Third, we indexed the shape of each forest structural class. Shape = 1 when the patch is square, and increases with irregularity. Additionally, given the strong relationship identified in Kosterman et al. (2018), we calculated the same mature forest connectivity index (MFICI) presented therein. The MFICI is effectively an “area-normalized correlation length,” whereby correlation length measures the average

extensiveness of connected patches (McGarigal et al., 2012). We expected the probability of litter production by a female to increase with mature and advanced regenerating forests because these structures produce the abundant and consistent snowshoe hares required by Canada lynx.

We used generalized linear mixed-models (GLMM; Bolker et al., 2009) and an information-theoretic approach (Burnham and Anderson, 2002) to characterize the relationship between litter production and forest structure. We used a binomial distribution (logit link) and included a random intercept to account for repeated measures of the same female over multiple years (Bolker et al., 2009). For each forest structural class, we identified the best (based on AIC_c) metric, scale (core use area, non-core area, or home range), and function (i.e., linear or curvilinear) associated with a female's proclivity to produce kittens. This resulted in four explanatory variables that were uncorrelated from one another ($|r| < 0.60$): (1) MFCI in core use areas, (2) clumpiness of advanced regeneration at the home range, (3) percentage of stand initiation at the core use area, and (4) percentage of sparse forest at the home range. We predicted that the MFCI (e.g., Kosterman et al., 2018) and patches of advanced regeneration arranged in a clumpy configuration would be positively associated with litter production by female lynx. Female lynx avoid sparse forest and stand initiation (Holbrook et al., 2017a), thus we expected a negative effect on litter production. We formalized these predictions within multiple competing hypotheses and evaluated support using AIC_c (Burnham and Anderson, 2002).

We evaluated the fit of our top model and assessed the sensitivity of litter production to changes in forest structure. As an assessment of fit, we calculated the marginal and conditional coefficient of determination (R^2_m and R^2_c , respectively; Nakagawa and Schielzeth, 2013). The marginal R^2 is the variance explained by only the fixed-effects, whereas the conditional R^2 is the variance explained by both fixed and random factors. This assessment allowed us to examine how each portion of the model (i.e., fixed and random) accounted for variation in the response of females producing litters of kittens.

To evaluate the sensitivity of litter production to changes in forest structure, we implemented a randomization procedure similar to Tempel et al. (2014). Our randomization process consisted of simultaneously drawing 1000 samples (with replacement) from the range of values (i.e., a uniform distribution) for each forest structure variable included in our top GLMM. Additionally, because we accounted for individual-level variation via a random intercept for female lynx, we also randomly sampled (with replacement) 1000 female labels. Randomizing the labels of female lynx allowed us to incorporate individual-level variation within our sensitivity analysis, rather than only assessing variation of the fixed factors (i.e., forest structure variables). For each of the 1000 samples, we applied our top GLMM model to generate 1000 probabilities of producing a litter. We then used linear regression and R^2 to characterize how variation in forest structure influenced the total variation in the probability of producing a litter of kittens. We conducted all analyses in program R (R Core Team, 2017).

2.4.2. Step two - characterizing forest mosaics across the gradient in female quality for forest management

We characterized the number and arrangement of core use units (within core areas) and calculated management-relevant metrics of forest structure across the gradient in female quality. First, we generated predicted probabilities of producing a litter of kittens for each female using our supported model(s), which we then used to classify females into three quantiles of reproductive quality (i.e., low, medium, and high). Second, for each female within each category of quality, we counted the number of core use units as well as estimated the average nearest neighbor distance between core use units. We expected high quality females to exhibit somewhat centralized core areas such that the number of units was lower and closer together when compared to low quality females. Finally, we summarized our predictions of forest structural classes (pixel-level from Savage et al., 2018) to the patch-level to more easily translate to management decision-making, which is often associated with the stand or patch. We used a polygon layer of forest patches that was developed using aerial imagery and eCognition® software (see Brown and Ahl, 2011), and we assigned the forest structural class that was observed most frequently to each polygon. We then calculated landscape metrics of forest structure using FRAGSTATS software (version 4.2; McGarigal et al., 2012) for each female and spatial scale: (1) percentage of the landscape (%), (2) median patch size (ha), (3) connectance (index), (4) clumpiness (index), and (5) shape (index). We described clumpiness and shape previously (Section 2.4.1). Connectance is an index (ranges between 0 and 100) that characterizes patch connectivity, where values of 0 indicate no patches are connected and values of 100 indicate all patches are connected (McGarigal et al., 2012). We applied an 8-cell patch rule for all calculations and searched a radius of 500 m to calculate connectance.

We believed our sample of female lynx included most individuals present in our survey areas based on field observations of track patterns and capture histories. Even so, because of the small number of females within each category of quality (i.e., 32 females in total), we assessed differences in core use areas and forest structure metrics using non-parametric summaries. For instance, we calculated the median and interquartile range (IQR) of each variable for each category of quality. If the IQR did not overlap the median value of another group, we concluded there was evidence of a difference. This was a conservative approach, because the median $\pm (1.57 \times \text{IQR}/\sqrt{n})$ is also used to assess differences among distributions (Chambers et al., 1983), which generally exhibits bounds narrower than the IQR.

3. Results

3.1. Forest structure and snowshoe hares

Consistent with our expectations, the proportion of sites occupied by snowshoe hares was higher in the advanced regeneration and mature structural classes (Fig. 2a). Occupancy of snowshoe hares was the

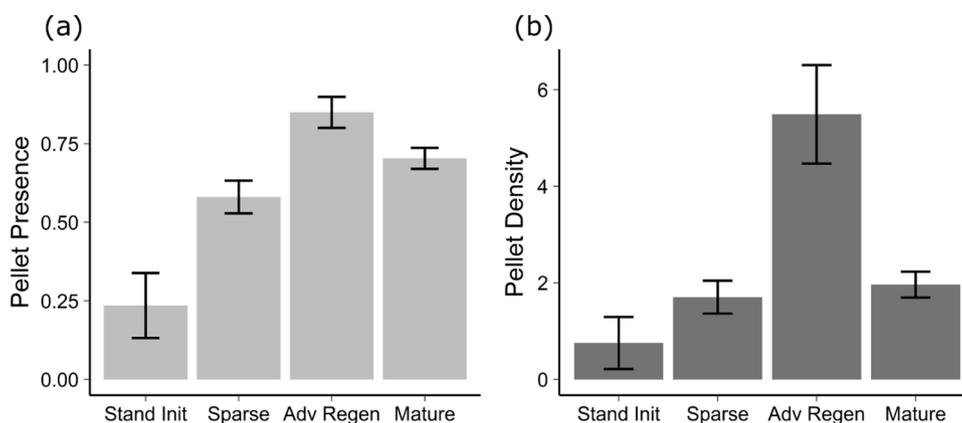


Fig. 2. Estimated (\pm 95% CIs) proportion of sites occupied (a) and relative density (b) of snowshoe hares (*Lepus americanus*) across our forest structural classes. Total sample size of plots 1340, which were distributed unevenly across forest classes: stand initiation ($n = 69$), sparse ($n = 348$), advanced regeneration ($n = 206$), and mature ($n = 718$).

lowest in stand initiation, followed by the sparse structural class (Fig. 2a). However, the relative density of snowshoe hares was ≥ 2.8 -times higher in the advanced regeneration structural class when compared to all other structural classes (Fig. 2b). The structural class that produced the next highest density of snowshoe hares was mature, followed by sparse and stand initiation (Fig. 2b).

3.2. Age distribution and transition times of forest structural classes

The age distributions of our forest structural classes followed our general expectations (Fig. 3). Most trees in stand initiation were young and between 0 and 19 years old (i.e., 30% of the distribution), but some occurred in older age classes as well. These plots tended to exhibit open canopies following timber harvest with some retained older trees, which was consistent with a median DBH of 0 in. (IQR = 0–8 in.) and 8% canopy cover (IQR = 0–36%; Fig. 3, Appendix A). We observed a diversity of tree ages in our sparse class (including ≥ 200 years old), but most trees (i.e., 72% of the distribution) were between the ages of 0–19 and 60–79 years old (Fig. 3). Median DBH and canopy cover for sparse

forest was 6 in. (IQR = 0–11 in.) and 28% (IQR = 8–49%), respectively (Appendix A). Tree ages within advanced regeneration exhibited a right-skewed distribution and most trees (i.e., 75% of the distribution) were between 0 and 19 and 60–79 years old (Fig. 3). Median DBH of advanced regeneration was 8 in. (IQR = 5–10 in.) and canopy cover was 45% (IQR = 30–70%). Lastly, the majority of trees (i.e., 66%) within mature forest were between 40 and 59 and 100–199 years old, however, 30% of the trees were classified as ≥ 120 years old (Fig. 3). Mature forest exhibited a median DBH of 10 in. (IQR = 7–14 in.) and 56% (IQR = 40–70%) canopy cover (Appendix A), which were higher than any other structural class. In addition, 21% of the trees within mature forest were 15–25 in. DBH, highlighting the multistoried nature of mature forests (Appendix A).

In the context of a forest reset (i.e., a clearcut), the temporal transitions between forest structural classes followed an intuitive progression. Stand initiation was the dominant structural class following regeneration cuts for ≈ 8 years post-harvest (Fig. 4). Sparse was the dominant structural stage during ≈ 9 –24 years post-harvest (Fig. 4), but throughout the time sequence sparse remained $\geq 30\%$ prevalent

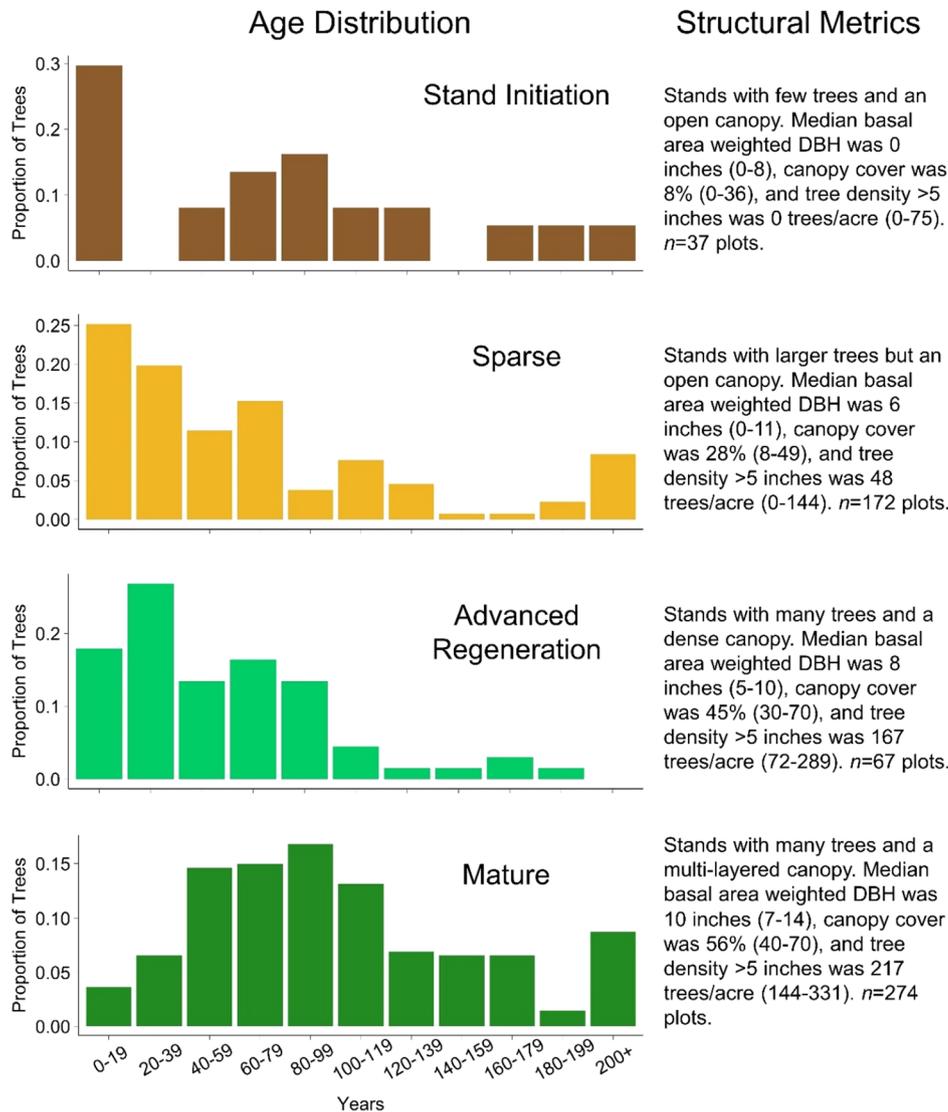


Fig. 3. Description of forest structural classes using subplot data ($n = 550$) from the USDA Forest Service Forest Inventory and Analysis (FIA) program that overlapped our mapped forest structural classes. We characterized the age distribution of our structural classes by plotting the proportion of trees within each age category. We summarized forest structural metrics (as measured via FIA) associated with our structural classes using median values (with IQR in parentheses). For an exhaustive list of forest structural metrics, please see Appendix A. Acronym DBH indicates the diameter at breast height. The calculation for basal area weighted DBH was as follows: $\Sigma(\text{tree Basal Area} \cdot \text{DBH}) / \text{Total Basal Area}$. Note the y-axis varies with respect to structural class.

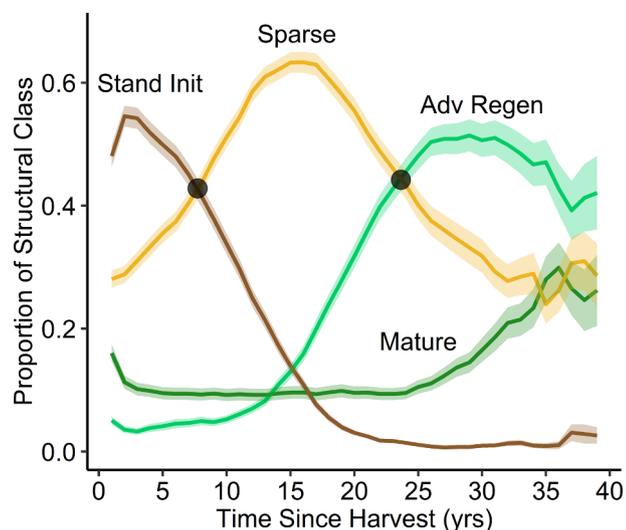


Fig. 4. Temporal transitions of forest structural classes in the context of a vegetation reset from a regeneration cut (e.g., a clearcut, $n = 791$) during 1973–2013 (i.e., 1–39 years post-harvest). Lines indicate mean proportions ($\pm 90\%$ CIs) and black dots indicate dominance transition points. The stand initiation class dominated during ≈ 1 –8 years post-harvest, followed by sparse and advanced regeneration. We did not observe the full time sequence required to develop elements of mature forest given our time series, indicating this class takes at least ≈ 50 years to begin establishing after a reset.

indicative of the many different forms of sparse forest (e.g., could be young or old). The advanced regeneration class was low for the first ≈ 15 years after harvest, after which it increased and dominated from ≈ 25 years post-harvest throughout the remaining portion of our time frame (i.e., 39 years; Fig. 4). We did not observe the time frame in which the mature structural class began to dominate, indicating that it takes at least ≈ 50 years or more for elements of a mature forest to develop (Fig. 4). This temporal context of successional changes associated with silviculture provides managers with the information necessary to develop harvest rotations.

3.3. Forest mosaics, core use areas, and female quality of Canada lynx

We monitored 32 females over the course of 92 potential reproductive events. Of those, we observed 62 litters of kittens, which resulted in an overall kitten production rate of 67%. The median home range size for females was 23 km² (range = 18–66 km²), while the median core use area was 6 km² (range = 3–21 km²).

The proclivity of female lynx to produce kittens was influenced by the amount and arrangement of forest structural classes in home ranges, especially in core use areas. Our results supported (i.e., $\Delta AIC_c \leq 2$) multiple models, but the top model (i.e., $\Delta AIC_c = 0$) suggested lynx were most influenced by the mature forest connectivity index (MFCI) and the percentage of the landscape that was stand initiation (Table 1). The regression coefficients (i.e., unstandardized) indicated that the effect of both explanatory variables were significant: $\beta_{MFCI} = 3.33$ (90% CI = 0.84–6.52) and $\beta_{StandInit} = 0.18$ (90% CI = 0.02–0.37). The effect of advanced regeneration was also included within the supported model set (Table 1), but the relationship was not statistically significant: $\beta_{AdvRegen} = 5.06$ (90% CI = -2.00 to 13.01). The marginal and conditional coefficient of determination from our top model was $R_m^2 = 0.15$ and $R_c^2 = 0.39$, respectively, which indicated substantial individual variation among female lynx in their ability to produce litters of kittens. Indeed, approximately 62% of the total variation explained (i.e., $(0.39-0.15)/0.39 = 62\%$) was attributed to among-individual variation. Furthermore, the null model that only incorporated the random effect of female lynx was within our supported set, once again suggesting considerable individual variation. Nevertheless, the marginal

Table 1

Models assessing the influence of forest structure and arrangement on the proclivity of female Canada lynx (*Lynx canadensis*) to produce litters of kittens. For each model, we provided the log-likelihood (LL), ΔAIC_c , and AIC_c weights (w). As a measure of fit, we calculated a generalized measure of R^2 from our top (i.e., $\Delta AIC_c = 0$) generalized linear mixed-model (Nakagawa and Schielzeth 2013). Our marginal (fixed factor variation) and conditional (total variation) estimates were $R_m^2 = 0.15$ and $R_c^2 = 0.39$, respectively. Abbreviation MFCI indicates the mature forest connectivity index. Metrics characterizing the proportion of the landscape (PLAND) and the clumpiness index (CLUMPY) were abbreviated.

Model Description	LL	ΔAIC_c	w
MFCI ^a + PLAND.Stand Initiation ^a	-51.60	0.00	0.27
MFCI	-53.27	1.09	0.16
Null	-54.63	1.67	0.12
MFCI + CLUMPY.Adv Regeneration ^b	-52.56	1.86	0.11
MFCI + CLUMPY.Adv Regeneration + PLAND.Stand Initiation	-51.56	2.09	0.10
MFCI + PLAND.Stand Initiation + PLAND.Sparse ^b	-51.60	2.19	0.09
MFCI + PLAND.Sparse	-53.22	3.17	0.06
MFCI + CLUMPY.Adv Regeneration + PLAND.Sparse	-52.14	3.26	0.05
MFCI + CLUMPY.Adv Regeneration + PLAND.Stand Initiation + PLAND.Sparse	-51.44	4.14	0.04

^a At the core use area.

^b At the home range.

effects of MFCI and the percent stand initiation were significant and accounted for the remaining 38% of the total variation explained.

Because it was inappropriate to model average regression coefficients derived from generalized linear models (Cade, 2015), we performed our sensitivity analysis with only our top model. This analysis provided a more resolved understanding concerning the relationship between forest structure and the probability of a female lynx producing a litter of kittens. Despite the statistical effect of both MFCI and percent stand initiation from our GLMM, our sensitivity analysis indicated that litter production was substantially more sensitive to changes in MFCI than the percent stand initiation per se (Fig. 5). For instance, the R^2 between MFCI and the probability of producing a litter was 0.30, while the R^2 associated with stand initiation was 0. However, it is important to note that as stand initiation increases within a core use area, mature forest will (at some point) by definition decrease resulting in a reduction of the MFCI. Although more sensitive to MFCI, our analysis further indicated that the probability of producing a litter varied substantially among female lynx (e.g., see spread in Fig. 5).

To assign our index of quality to each female lynx, we averaged the predicted probabilities of producing a litter across our model set, which is an appropriate technique to incorporate prediction uncertainty (rather than averaging model coefficients and subsequently generating predictions; Cade, 2015). The averaged predicted probabilities of producing a litter of kittens ranged from 0.30 to 0.92 across the 32 females. This resulted in the following categorization of females into low, medium, and high quality: low quality probabilities = 0.30–0.51 ($n = 10$ females), medium quality probabilities = 0.60–0.80 ($n = 11$ females), and high quality probabilities = 0.81–0.92 ($n = 11$ females).

The number and arrangement of core use units within core areas was generally similar across the gradient in female quality (Table 2, Fig. 6). Females exhibited ≈ 2 –5 spatially separate units within core use areas irrespective of the ability for females to produce kittens. Further, the average nearest neighbor distance between core use units was similar (≈ 1600 m) between low and medium quality female lynx (Table 2). However, there was evidence suggestive of high quality females having more spatially centralized core areas based on their lower nearest neighbor distance among core use units (≈ 1100 m; Table 2) when compared to medium quality females, providing some support for our predictions.

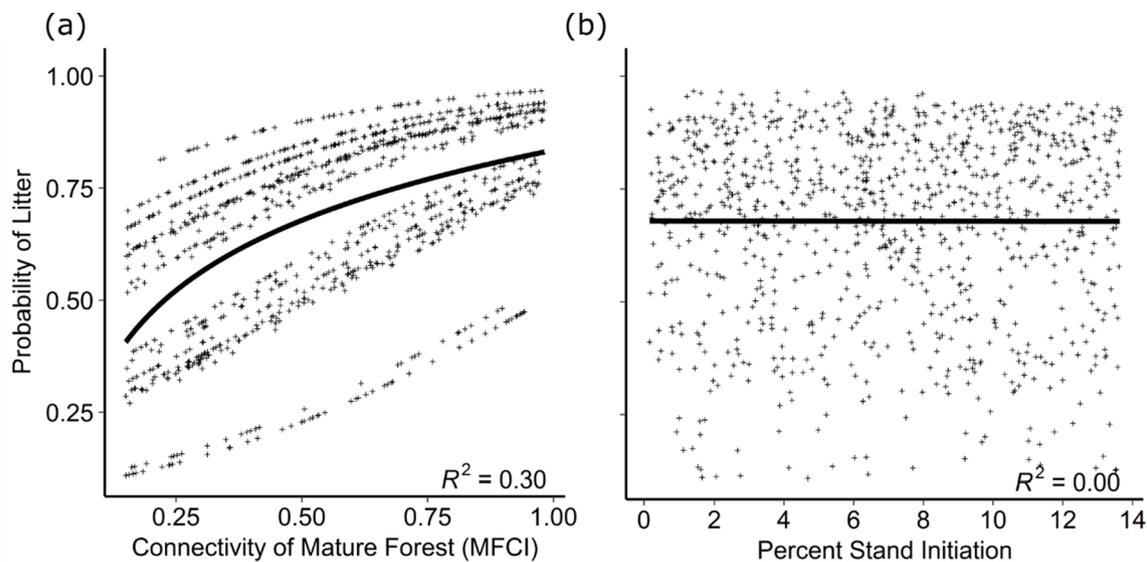


Fig. 5. Sensitivity of litter production by female Canada lynx (*Lynx canadensis*) to changes in forest structure. Each data point represents one realization of 1000 randomizations of mature forest connectivity (at the core use scale), percent stand initiation (at the core use scale), and the identity of female lynx: (a) indicates a log-linear relationship between the variation in mature forest connectivity index (MFCI) and the probability of producing a litter, (b) indicates no relationship between the variation in percent stand initiation and the probability of producing a litter.

Table 2

Median (M) and interquartile range (IQR) of the number of core use units and average nearest neighbor distance among core use units within core areas across our gradient of female quality for Canada lynx (*Lynx canadensis*). Female quality was based on their probability of producing a litter of kittens: low quality = probability of litter 0.30–0.51 ($n = 10$), medium quality = probability of litter 0.60–0.80 ($n = 11$), and high quality = probability of litter 0.81–0.92 ($n = 11$).

Female Quality	Characteristics of Core Use Areas	
	Number of spatial units	Distance between spatial units (m)
Low	M: 2.5 IQR: 2–4	M: 1571 IQR: 435–2670
Med	M: 3 IQR: 1.5–6	M: 1705 IQR: 280–2464
High	M: 3 IQR: 2–4.5	M: 1108 IQR: 640–1682

To summarize differences in forest structure and arrangement across categories of female quality, we focused on comparisons between low and high quality females (Table 3, Fig. 7, Appendix B). Of these comparisons, we found that forest structure in core use areas distinguished female quality more than the overall home range. For instance, we observed differences across classes of female quality within core use areas 70% of the time, versus 30% and 50% of the time at non-core use areas and home ranges, respectively (Table 3, Appendix B). Thus, the abundance and arrangement of structural classes in core use areas had the greatest influence on reproductive success for female Canada lynx.

Low quality and high quality female Canada lynx exhibited differences in many metrics of forest structure. Mature forest was 17% more abundant (median = 58%, IQR = 55–65%) and was more connected, less clumpy, and exhibited 2.25-times larger patch sizes in core use areas of high quality females compared to low quality females (Table 3, Figs. 7, 8, Appendix B). Indeed, mature forest was 2.5-times more abundant than any other structural class in the core use areas of high quality females (Table 3). The abundance, patch size, and connectance of mature forest were all higher at the core use area than at the non-core area (Table 3, Figs. 7, 8). These differences indicated the distinctiveness of core use areas and the importance of mature forest as the landscape matrix.

We discovered differences between low and high quality females for the remaining forest structural classes as well. High quality females exhibited 3% more stand initiation (median = 4%, IQR = 2–6%) and 8% less advanced regeneration (median = 18%, IQR = 12–24%) along with 14% less sparse forest (median = 23%, IQR = 17–24%) than did low quality females (Table 3). Further, high quality females displayed smaller patches of advanced regeneration and larger patches of sparse forest when compared to low quality females (Figs. 7, 8, Appendix B). The clumpiness and connectance of sparse forest were both lower for high quality females than low quality females. However, patches of advanced regeneration were clumpier and more connected for high quality females (Figs. 7, 8, Appendix B). Lastly, patches of sparse forest were more irregularly shaped in core areas of low quality females relative to high quality females. We observed no differences in the remaining comparisons within core use areas of female lynx.

4. Discussion

Our objective was to inform the intersection of forest management and Canada lynx conservation by providing detailed information characterizing high quality habitat. We confirmed (similar to Kosterman et al., 2018) that core use areas (3–21 km²), which can be one spatial unit or many (Figs. 6, 8), are more important than aspects of the entire home range (18–66 km²) for litter production by female Canada lynx. This does not, however, mean that home ranges of female lynx are unimportant, and indeed home ranges are by definition a defended area that females have chosen to occupy. Further, all categories of female quality exhibited a similar number of spatial units within core use areas, and there was only moderate support for units closer together within high quality females. We discovered that the productivity of females was most sensitive to the connectivity of mature, multistoried forests (composed of mostly spruce-fir) within core use areas, but litter production also varied substantially among females (i.e., 62% of the variation explained) for reasons we did not measure. Mature forest was more abundant, connected, and exhibited 2.25-times larger patch sizes in core areas of high quality females versus low quality females. The positive relationship between litter production and the connectivity of mature forest was likely a result of mature forest providing temporally consistent and accessible snowshoe hares as prey (e.g., Griffin and Mills, 2009; Squires et al., 2010; Ivan et al., 2014; Ivan and Shenk,

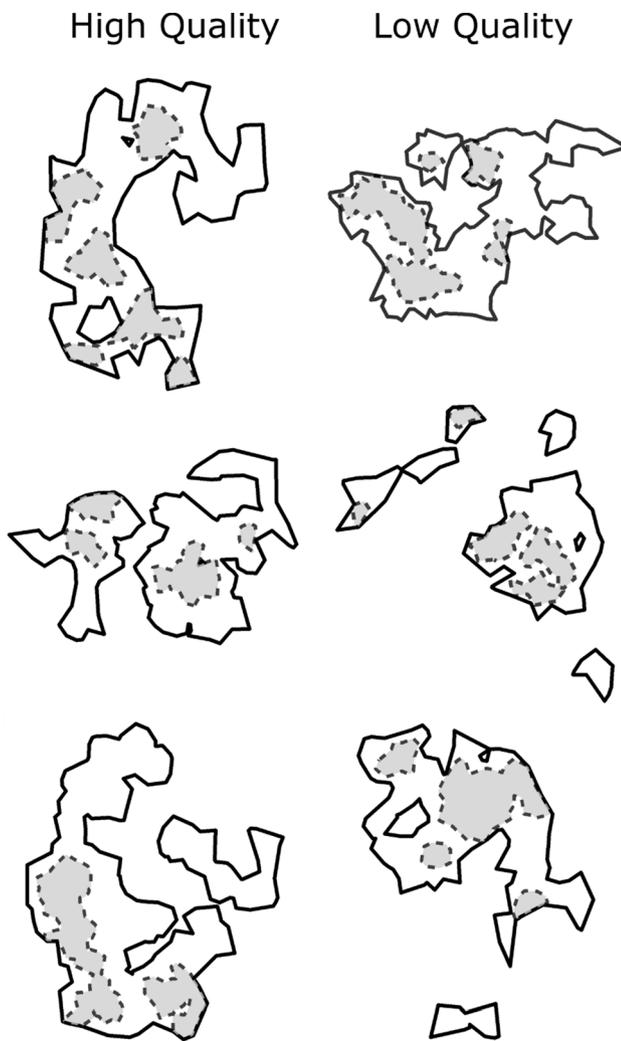


Fig. 6. Example core use areas (gray areas), within home ranges (solid black outline), demonstrating the similarity in number and arrangement of core areas between high and low quality female Canada lynx (*Lynx canadensis*). Core areas indicated the 50% isopleth of a female's home range while a home range was the 90% isopleth. Quality of females was determined based on their probability of producing a litter of kittens, which resulted in the following: low quality = probability of litter 0.30–0.51 ($n = 10$), medium quality = probability of litter 0.60–0.80 ($n = 11$), and high quality = probability of litter 0.81–0.92 ($n = 11$). All females presented had ≥ 500 GPS locations to characterize the home range and core use area.

2016). The advanced regeneration structural class supported the highest relative density of snowshoe hares compared to other structure classes (Fig. 2), but this class only occurs for ≈ 80 years (Fig. 3) and lynx may have difficulty capturing hares in advanced regeneration because of dense vegetation (e.g., Fuller et al., 2007; Ivan and Shenk, 2016). Thus, a high quality home range for female Canada lynx is best characterized as a landscape mosaic with abundant (e.g., ≈ 50 –60%) and connected mature, multistoried forest with intermediate amounts (e.g., ≈ 18 –19%) of advanced regeneration (e.g., Table 3, Figs. 7, 8). Managers can use our assessments of snowshoe hare density, forest ages and transition times, and habitat quality of Canada lynx to guide spatio-temporal decisions that aid in the conservation of lynx in the Northern Rockies through increased kitten production. Collectively, our work represents an important step in narrowing the gap between forest management and the conservation of threatened and endangered species.

4.1. Habitat-fitness relationships of Canada lynx

We confirmed the conclusion of Kosterman et al. (2018) that the probability of Canada lynx producing a litter of kittens increased with both the connectivity of mature forest and the abundance of stand initiation in core areas. However, we expanded this understanding by highlighting that variation in litter production was more sensitive to the connectivity of mature forest, rather than the abundance of stand initiation (Fig. 5); although, at some point increasing stand initiation will by definition decrease the connectivity of mature forest. A pattern similar to ours was discovered in cheetahs, where cub recruitment was 1.79 times higher when females occupied dense habitat relative to open habitats (Broekhuis, 2018). We also highlighted that the probability of producing a litter varies substantially among female Canada lynx independent of forest structure, which indicated innate or unmeasured variation associated with females or habitat were also important drivers of their ability to produce litters.

Many studies have highlighted the important role of maternal experience, reproductive history, and condition on female reproductive success (e.g., Monteith et al., 2013; Gaillard et al., 2014; Rauset et al., 2015). For example, Gaillard et al. (2014) demonstrated that maternal experience in female Eurasian lynx was important for both producing a litter of kittens as well as the number of kittens recruited. However, in a previous study on the same population of Canada lynx in the Northern Rockies, Kosterman et al. (2018) documented that habitat attributes were more important drivers of kitten production than maternal age, reproductive status (i.e., litter present/absent) in the previous year, or physical condition (as indexed via body mass and length). Thus, the residual variation we observed in reproductive success for adult female lynx might be associated with (1) stochastic variation in prey availability during the breeding season, causing females to forgo reproduction (e.g., Brand and Keith, 1979; Parker et al., 1983), or (2) other unmeasured factors such as individual variation in dominance, stress, or rearing behavior (e.g., Champagne et al., 2003; Murray et al., 2007; Sheriff et al., 2009). Nevertheless, our results suggest that forest managers have an opportunity to improve the reproductive performance of female Canada lynx by altering forest structure, but with the understanding that other factors also drive demography given the among-female variation we observed (e.g., Fig. 5).

Applying our insights, we were able to characterize the management-relevant components of high quality habitat for Canada lynx in the Northern Rockies (e.g., Fig. 7, Table 3). Core use areas are an important feature within the greater home range for female lynx. However, rather than characteristics of the core area itself, such as the number of spatial units representing the core or the distance between those units (Table 2, Fig. 6), it is the composition and arrangement of forest structural classes that distinguishes the core. This is similar in concept to grizzly bear (*Ursus arctos*) core areas in that they are defined based on road densities, which negatively influences adult survival, juvenile recruitment, and population growth (e.g., Boulanger and Stenhouse, 2014). In our case, mature forest was more abundant within core areas of high quality female lynx, and patches of mature forest were larger and more connected than the non-core portion of lynx home ranges (Figs. 7, 8, Table 3, Appendix B). Therefore, both core use areas and the greater home range are important constructs when implementing management actions aimed at Canada lynx conservation. The core use areas of high quality females exhibited the following structural compositions (i.e., medians and IQR from Table 3): mature = 58% (IQR = 55–65%), advanced regeneration = 18% (IQR = 12–24%), sparse = 23% (IQR = 17–24%), and stand initiation = 4% (IQR = 2–6%). At the home range level, the composition of forest structural classes included: mature = 49% (IQR = 43–59%), advanced regeneration = 19% (IQR = 14–24%), sparse = 26% (IQR = 18–30%), and stand initiation = 5% (IQR = 3–6%). While these numbers improve the understanding of Canada lynx habitat quality in the Northern Rockies, it is important to recognize that these

Table 3
 Median (M), interquartile range (IQR), and range (R) of the percentage of forest structural classes at three spatial scales (Core Area, Non-Core, and Home Range, whereby Home Range = Core + Non-Core) across our gradient of female quality for Canada lynx (*Lynx canadensis*). Female quality was based on their probability of producing a litter of kittens: low quality = probability of litter 0.30–0.51 (n = 10), medium quality = probability of litter 0.60–0.80 (n = 11), and high quality = probability of litter 0.81–0.92 (n = 11). For additional descriptions of forest structure see Appendix A. Tree species abbreviations include: PIEN - Engelmann spruce (*Picea engelmannii*), ABLA - subalpine fir (*Abies lasiocarpa*), PICO - lodgepole pine (*Pinus contorta*), LAOC - western larch (*Larix occidentalis*), and PSME - Douglas fir (*Pseudotsuga menziesii*).

Structural class	General description	Core Area			Non-Core			Home Range		
		Low	Medium	High	Low	Medium	High	Low	Medium	High
Stand Initiation	Mixed species stands (include PIEN-ABLA, PICO, LAOC, and PSME) that have few trees, an open canopy, and are often a result of recent disturbance	M: 1% IQR: 0–4 R: 0–5	M: 0% IQR: 0–4 R: 0–13	M: 4% [†] IQR: 2–6 R: 0–8	M: 2% IQR: 0–5 R: 0–8	M: 1% IQR: 0–5 R: 0–13	M: 4% IQR: 1–6 R: 0–31	M: 2% [‡] IQR: 1–4 R: 0–7	M: 1% IQR: 0–1 R: 0–13	M: 5% IQR: 3–6 R: 0–16
Sparse	Stands dominated by PIEN-ABLA (followed by PSME, PICO, and LAOC) that are sparsely stocked (naturally) or mechanically thinned, which tend to be younger but could occur at any age	M: 37% IQR: 21–44 R: 13–48	M: 28% IQR: 21–41 R: 16–50	M: 23% [§] IQR: 17–24 R: 9–38	M: 29% IQR: 20–33 R: 11–65	M: 28% IQR: 20–33 R: 16–58	M: 26% IQR: 20–33 R: 9–41	M: 34% IQR: 25–38 R: 12–61	M: 26% [§] IQR: 20–35 R: 16–55	M: 26% [§] IQR: 18–30 R: 9–33
Advanced Regeneration	Stands dominated by PIEN-ABLA (followed by PICO, PSME, and LAOC) and exhibit a dense canopy and understory.	M: 26% IQR: 10–36 R: 6–46	M: 18% IQR: 11–32 R: 2–42	M: 18% [§] IQR: 12–24 R: 5–29	M: 16% IQR: 12–22 R: 6–42	M: 18% IQR: 10–27 R: 4–45	M: 20% IQR: 15–25 R: 5–38	M: 17% IQR: 12–26 R: 6–43	M: 23% IQR: 10–25 R: 3–44	M: 19% IQR: 14–24 R: 6–35
Mature	Stands arranged in a multi-storied structure (i.e., uneven age distribution) with a dense canopy and understory. Dominated by PIEN-ABLA (followed by PICO, PSME, and LAOC)	M: 41% IQR: 35–43 R: 22–69	M: 46% IQR: 31–63 R: 9–73	M: 58% [†] IQR: 55–65 R: 32–69	M: 45% IQR: 43–54 R: 16–73	M: 47% IQR: 36–62 R: 11–77	M: 48% IQR: 38–60 R: 23–72	M: 43% IQR: 39–46 R: 21–71	M: 53% IQR: 31–61 R: 10–75	M: 49% [†] IQR: 43–59 R: 30–70

[†] Higher than low quality female.

[§] Lower than low quality female.

[‡] Lower than high quality female.

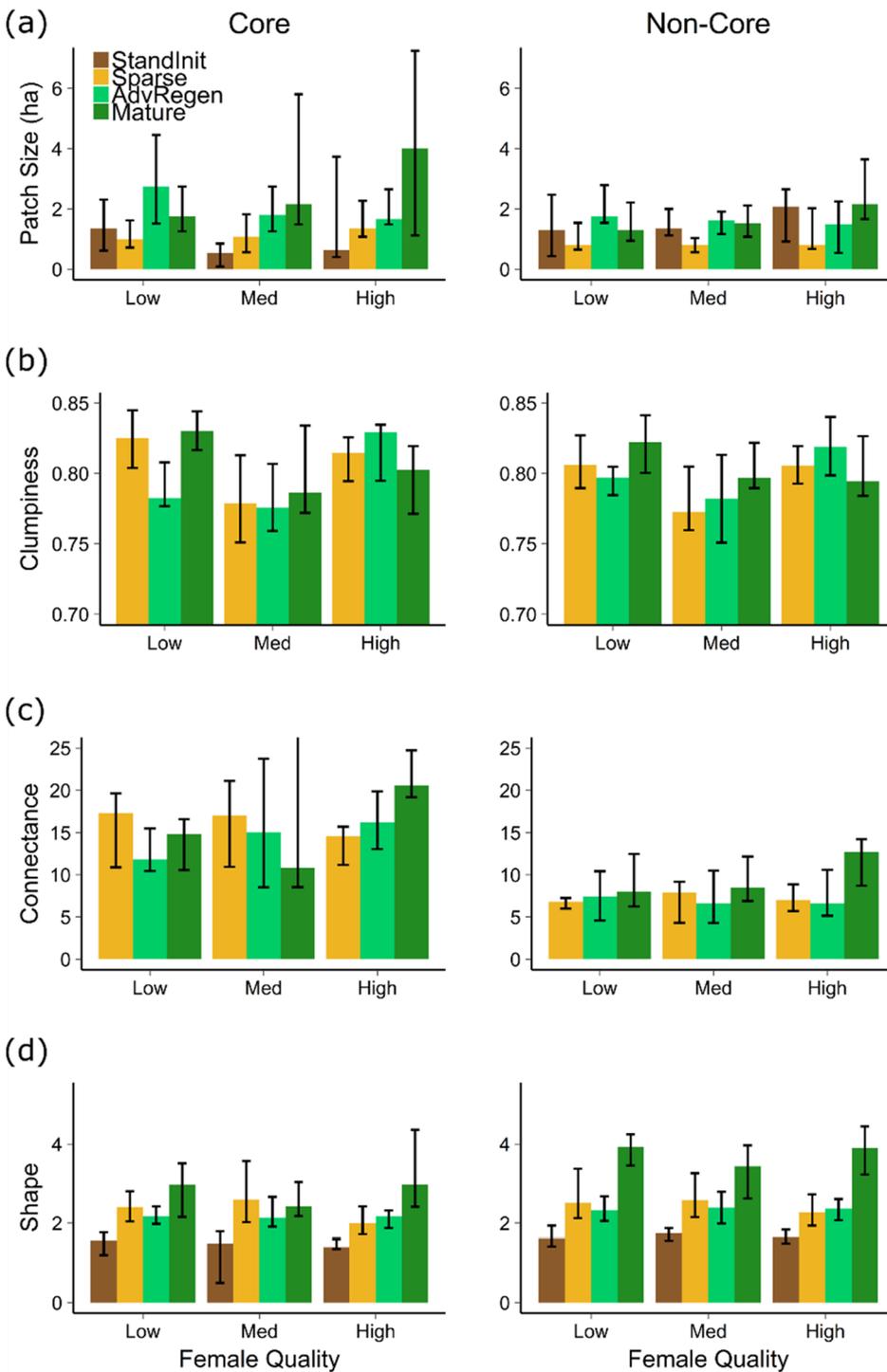


Fig. 7. Patch metrics of forest structural classes across a gradient in reproductive quality of female Canada lynx (*Lynx canadensis*). Core indicates the 50% isopleth of a female’s home range, and Non-Core represents the area outside of the core but within a 90% home range. This figure shows the median patch size (a), clumpiness (b), connectance (c), and shape (d) of forest structure patches. We removed stand initiation from (b) and (c) because of substantial variation given the small number and physical size of patches (e.g., see patch sizes in a); however, values for stand initiation are presented in Appendix B. Error bars indicate the interquartile range. Quality of females was determined based on their probability of producing a litter of kittens, which resulted in the following: low quality = probability of litter 0.30–0.51 ($n = 10$), medium quality = probability of litter 0.60–0.80 ($n = 11$), and high quality = probability of litter 0.81–0.92 ($n = 11$).

values are approximate and (as with all models) include error from the initial modeling of forest structural classes in Savage et al. (2018). Therefore, these numbers should be used in a general sense and in combination with previous work in the Rocky Mountains (e.g., Squires et al., 2008, 2010; Ivan and Shenk, 2016), which would be most appropriately applied in field evaluations of habitat on-the-ground.

The characteristics of a high quality home range aligned with multi-scale habitat selection of Canada lynx, suggesting a link between behavior and fitness (e.g., observed elsewhere in wild dogs; Davies et al., 2016 and gray wolves; Ubani et al., 2017). For instance, at a landscape-scale, lynx in the Northern Rockies generally select home ranges with abundant mature forest and intermediate amounts of advanced

regeneration (Holbrook et al., 2017a). Within their home ranges, lynx strongly select (i.e., use relative to random expectation) advanced regenerating forest (Holbrook et al., 2017a) suggesting a landscape mosaic that is compatible with forest management. Similar to Griffin and Mills (2009), our analyses indicate that mature, multistoried forests provide spatially consistent snowshoe hares (e.g., Fig. 2a) that are likely accessible for lynx (e.g., Squires et al., 2010; Ivan and Shenk, 2016) over a temporal gradient of ≈ 50 to > 200 years (e.g., Fig. 3). Advanced regeneration provides the highest densities of snowshoe hares (e.g., Fig. 2b), but over a narrower temporal window (e.g., ≈ 20 to 80 years; Figs. 3, 4) than mature forest. We speculate that snowshoe hares might also be more difficult to capture within the advanced

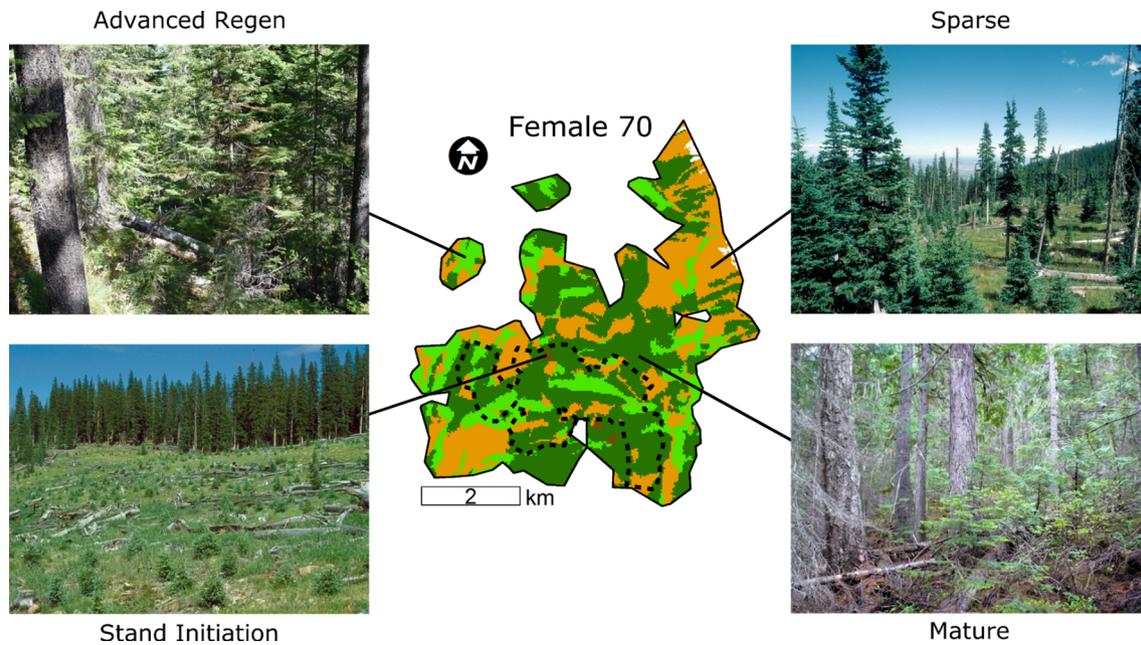


Fig. 8. Example of forest structural classes and arrangement in the home range and core use area (dashed line) of a high quality female Canada lynx (*Lynx canadensis*) in northwestern Montana, U.S. Female 70's probability of producing a litter of kittens was 0.92; indeed, she produced 7 litters of kittens out of 7 years of monitoring during 2001–2007. This example illustrates that a home range for a productive female includes a mosaic of structure classes from forest management, and that a core-use area (50% of use) is characterized by mature patches of forest with high connectivity. Photo credits: U.S. Forest Service.

regeneration structural class (e.g., Fuller et al., 2007; Ivan and Shenk, 2016) compared to other structural classes. Thus, a home range mostly composed of mature forest with islands of advanced regeneration appears to create an energetically efficient landscape for lynx to encounter and capture snowshoe hares, which are a critical resource for successful reproduction by lynx (e.g., Mowat et al., 1996; Slough and Mowat, 1996; O'Donoghue et al., 1997). Collectively, patterns of habitat selection and reproductive success of female Canada lynx in the Northern Rockies supports the theory of hierarchical behavior-fitness relationships (Rettie and Messier, 2000), which suggests limiting resources (e.g., mature, multistoried forest) drive broad-scale decisions, whereas finer-scale decisions (e.g., selection of advanced regeneration) enhance components of fitness.

4.2. Forest management and long-term conservation of Canada lynx habitat

The goal of our work was to evaluate and characterize habitat mosaics that contributed to the conservation of Canada lynx in the Northern Rockies over the long term. If the objective of forest management was to develop a framework that facilitated and sustained home ranges (e.g., 18–66 km² in size) and core use areas (3–21 km² in size) of high quality female lynx (e.g., Figs. 6, 8), our results provide many insights to such a framework (i.e., Fig. 9). However, it is important to note that our results are relevant to the home range extent (e.g., Fig. 8) and exhibit error that is customary in all studies that leverage satellite-derived predictions of the environment (e.g., forest structural class in our case). Therefore, our results and insights do not preclude field assessments of forest condition and would be best applied alongside previous work that precisely measured attributes of forest structure (e.g., tree sizes, canopy cover, tree densities) and horizontal cover in the field at locations used by lynx (e.g., Squires et al., 2008, 2010) and with high densities of snowshoe hares (e.g., Berg et al., 2012; Ivan et al., 2014; Holbrook et al., 2017b).

At the home range extent, our work informs forest management aimed at improving habitat quality of Canada lynx in the Northern Rockies (i.e., desired outcome in Fig. 9). In general, to enhance the reproductive success of female lynx, the desired condition is a

landscape dominated by abundant and well-connected mature, multi-storied forests (Squires et al., 2010; Holbrook et al., 2017a; Kosterman et al., 2018, this study) composed primarily of Engelmann spruce and subalpine fir (Squires et al., 2010; Holbrook et al., 2017a) within a habitat mosaic of forest structure that includes patches of advanced regeneration. A forest-management framework and silvicultural system that enhances this desired condition furthers Canada lynx conservation in the Northern Rockies.

To operationalize a framework for forest management, we propose implementing a series of steps. The first step would likely be an assessment of forest structural classes across a landscape of interest that is approximately the size of a female's home range. An important initial question would be, “does the landscape contain levels of mature, spruce-fir forest ($\approx 50\text{--}60\%$) and advanced regeneration ($\approx 18\text{--}19\%$) that increase habitat quality for female Canada lynx and provide abundant snowshoe hares (Fig. 9)?” This question focuses on mature, multistoried forest and advanced regeneration as the desired elements of lynx habitat. The values we suggested for mature forest (i.e., $\approx 50\text{--}60\%$) are conservative in that $\approx 60\%$ was from the core use area and $\approx 50\%$ was from the home range (Table 3). We suggest applying our core use and home range data together, because without location information for female lynx it would be impossible to identify core use areas (e.g., see complexity in Fig. 6). Furthermore, our focus on advanced regenerating and mature forests as the important components of lynx habitat is consistent with our work here, as well as other previous studies. For instance, male and female Canada lynx in the Northern Rockies select and defend home ranges that contain abundant mature, multistoried forests (e.g., Squires et al., 2008, 2010; Holbrook et al., 2017a). Additionally, at both the home range and within home range extent, male and female lynx select advanced regenerating forests and consistently avoid sparse and stand initiation structures (Squires et al., 2013; Holbrook et al., 2017a). Given this wealth of confirmatory information, we suggest forest managers focus on advanced regeneration and mature forest structures when efforts are aimed at improving habitat quality for Canada lynx.

Depending on the answer to the initial overarching question, there are many considerations relevant to management actions (Fig. 9). If the

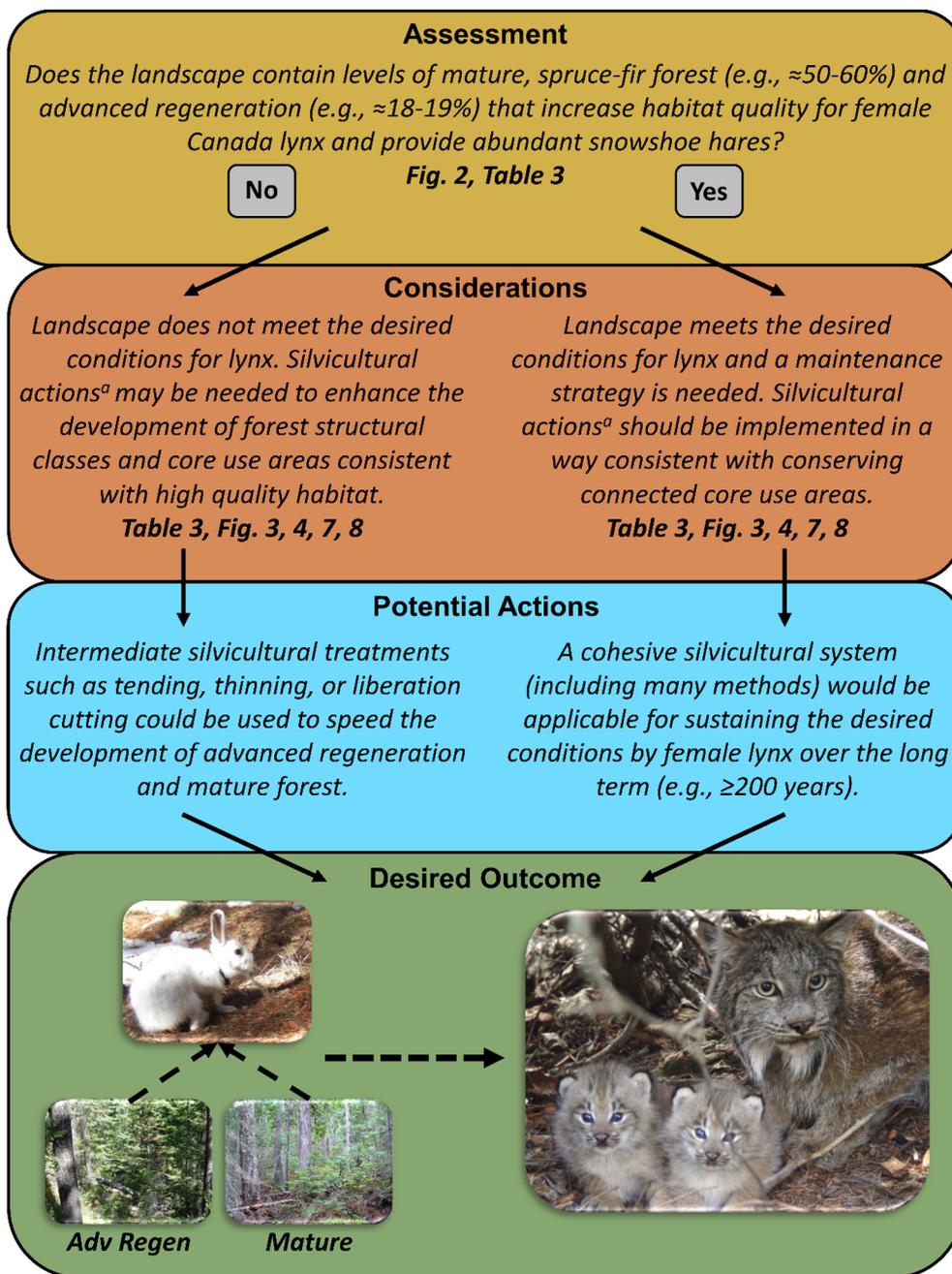


Fig. 9. Example management framework (with reference to helpful in-text information in **bold**) with the desired outcome of conserving high quality habitat for Canada lynx (*Lynx canadensis*) and abundant snowshoe hares (*Lepus americanus*) on multiple-use lands in the Northern Rockies, U.S. We defined high quality habitat based on the consistency of a female Canada lynx to produce a litter of kittens. The framework includes (1) an initial landscape assessment at the *home-range extent* followed by (2) a set of management considerations and (3) potential silvicultural actions, which ideally lead to (4) the desired outcome of a habitat mosaic conducive to providing snowshoe hares (*Lepus americanus*) and increasing the reproductive success of female Canada lynx. Superscript ^a indicates Holbrook et al. (2018) as a reference for discussing lynx responses to silvicultural treatments. Advanced regeneration is abbreviated by Adv Regen. Photo credit: U.S. Forest Service and Rocky Mountain Research Station, Northern Rockies Lynx Project.

answer is “no,” and the area does not meet the desired condition for female Canada lynx, then management actions may be warranted to increase the developmental rate of advanced regeneration (age distribution ≈ 20 – 80 years old) or mature forest (age distribution ≈ 50 - ≥ 200 years old). In the context of a vegetation reset, we demonstrated it takes at least ≈ 25 years for attributes of the advanced regeneration structure to begin developing and at least ≈ 50 years for elements of a mature forest (Fig. 4). However, intermediate silvicultural treatments (e.g., tending, thinning, or liberation cuts) might decrease the time required to establish attributes of either advanced regenerating or mature forests (Holbrook et al., 2018). If the answer is “yes” to the aforementioned question, and the landscape of interest meets the desired conditions for female Canada lynx, then a maintenance strategy might be warranted (Fig. 9). Implementing a long-term (e.g., > 200 years) and cohesive silvicultural system (including methods such as intermediate treatments and regeneration harvests) could be used to maintain the structural composition and arrangement given the

temporal (Figs. 3, 4) and spatial (Table 3, Appendix B) characteristics of forest structures we have characterized. However, balancing the short-term avoidance of Canada lynx to silvicultural treatments (Holbrook et al., 2018) with the long-term benefits would be an essential component to the silvicultural strategy, particularly given the threatened status of Canada lynx in the contiguous U.S.

5. Conclusion

Managing forests occupied with threatened and endangered species is a difficult task that requires balancing multiple objectives. This difficulty is compounded when it is unclear what habitat attributes are important for a species’ survival and reproduction. Here, we provided many advances characterizing habitat attributes important for the reproductive success of female Canada lynx in the Northern Rockies. While our assessment focused on reproduction, we do not diminish the importance of survival. Indeed, survival is required for continued

reproduction and our conclusions assume high female survival. We reinforced the findings of [Kosterman et al. \(2018\)](#) that core use areas within a home range context (see [Figs. 6, 8](#)) are a unique and important component for successful reproduction, although substantial residual variation exists among female lynx. Further, we demonstrated that (1) the probability of producing kittens by female lynx was most sensitive to the connectivity of mature, multistoried forests (composed of mostly spruce-fir), (2) the relative density of snowshoe hares was ≥ 2.8 times higher in advanced regenerating stands relative to other forest structures, including mature forest, (3) the home range ($\approx 18\text{--}66\text{ km}^2$) and core use area of high quality females was composed of $\approx 50\text{--}60\%$ mature forest and $\approx 18\text{--}19\%$ advanced regeneration, and (4) advanced regenerating and mature forests were $\approx 20\text{--}80$ years old and ≈ 50 to ≥ 200 years old, respectively, highlighting the developed nature of high quality Canada lynx habitat. This essential information, coupled with how lynx respond to silvicultural treatments ([Holbrook et al., 2018](#)), allows forest managers to develop and apply strategies that incorporate forest management and lynx conservation over the long term within a multiple-use context (e.g., [Fig. 9](#)).

However, one of the most difficult challenges currently facing forest management in the western U.S. is increasing wildfire seasons and activity (e.g., [Westerling et al., 2006](#); [Abatzoglou and Williams, 2016](#); [Westerling, 2016](#)). Increasing wildfire also complicates the conservation of high quality Canada lynx habitat because quality habitat contains older forest structures and, thus, relatively high fuel loads. Therefore, an important step forward for Canada lynx conservation will be evaluating forest management alternatives that are capable of balancing wildfire risk and the conservation of lynx habitat. Indeed, continuing to assess knowledge gaps at the intersection of forest management, natural and anthropogenic disturbance, and species conservation will be essential for future conservation efforts on western forests.

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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.2019.01.011>.

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