

Grizzly bear selection of recently harvested forests is dependent on forest recovery rate and landscape composition

Sean P. Kearney^{a,*}, Nicholas C. Coops^a, Gordon B. Stenhouse^{b,c}, Scott E. Nielsen^d, Txomin Hermosilla^e, Joanne C. White^e, Michael A. Wulder^e

^a University of British Columbia, Forest Resources Management, 2424 Main Mall, Vancouver, BC V6T 1Z4, Canada

^b fRI Research, 1176 Switzer Drive, Hinton, AB T7V 1V3, Canada

^c University of Saskatchewan, Western College of Veterinary Medicine, 52 Campus Drive, Saskatoon, SK S7N 5B4, Canada

^d University of Alberta, 2-06 Agriculture Forestry Centre, Edmonton, AB T6G 2P5, Canada

^e Canadian Forest Service (Pacific Forestry Centre), Natural Resources Canada, 506 Burnside Road West, Victoria, BC V8Z 1M5, Canada



ARTICLE INFO

Keywords:

Ursus arctos
Landsat
Habitat selection
Forest recovery
Forest disturbance
Time series
Spectral recovery

ABSTRACT

Forests in the early stages of regeneration are valuable habitat for threatened grizzly bear (*Ursus arctos*) populations inhabiting the interior mountains of North America, with forest management affecting the timing, prevalence, and quality of such habitats. Forest harvesting can lead to early-seral habitat, however the quality and duration of post-harvest habitat compared to natural disturbances (e.g., wildfire), is not known. North American silvicultural practices are mandated to ensure tree regrowth following harvesting, and a rapid rate of growth in managed tree regeneration may lead to a shorter time window during which attractive early-seral habitat is available to bears compared to natural forest disturbances. The distribution of natural disturbances across forested landscapes may also be an important consideration in the response of bears to forest harvesting. In this study, we analyzed grizzly bear habitat selection for 160 collared grizzly bears across 118,000-km² (68% of their known habitat) in Alberta, Canada, using metrics of forest disturbance and recovery derived from a 33-year satellite time series. We developed seasonal resource selection functions to evaluate (1) if selection of recently harvested forests was contingent upon the availability of natural disturbances, (2) how habitat selection within disturbed areas varied across disturbance types, and (3) how habitat suitability changed over time during the first 30 years of forest recovery following various disturbance types. Results showed that, compared to areas not recently disturbed, grizzly bears were up to three times more likely to select for harvested forests when natural disturbances were limited in their home range, while selection of harvested forests was neutral when natural disturbances were abundant. When available, grizzly bears were more likely to select for natural disturbances compared to harvested locations, especially during Hypophagia (spring) and Hyperphagia (fall). Selection of harvested locations was inversely related to forest recovery assessed by spectral analysis and decreased sharply 15–20 years post-harvest, at which point it tended to be lower than pre-disturbance. This study demonstrates the utility of vegetation, disturbance, and recovery metrics derived from satellite time series for enriching our understanding of wildlife habitat selection in dynamic landscapes. Our results also have implications for forest management in regions where grizzly bear habitat availability and selection patterns are important. While rapid forest recovery following harvest is desirable and beneficial for a multitude of ecological and economic objectives, it appears to minimize the period of attractive early-seral habitat for grizzly bears.

1. Introduction

Habitat loss is one of the primary concerns for sustaining wildlife populations, especially for threatened large carnivores such as grizzly (brown) bears (*Ursus arctos*). High energetic demands and low population densities of large carnivores tend to result in wide-ranging

behaviour, increasing the likelihood of interaction and conflict with humans (Ripple et al., 2014). Habitat loss and degradation, combined with direct mortality caused by humans, has contributed to steep population declines and historical range contractions for large carnivores in general (Ripple et al., 2014), and specifically for grizzly bears in the interior mountains of North America (Mattson and Merrill, 2002;

* Corresponding author.

E-mail address: sean. Kearney@alumni.ubc.ca (S.P. Kearney).

<https://doi.org/10.1016/j.foreco.2019.117459>

Received 21 February 2019; Received in revised form 4 July 2019; Accepted 5 July 2019

Available online 17 July 2019

0378-1127/ © 2019 Elsevier B.V. All rights reserved.

McLellan et al., 1999). Enhanced habitat quality can augment the resilience of bear populations through increased population density (Lamb et al., 2018; Mowat et al., 2005; Nielsen et al., 2016), improved body condition (Boulanger et al., 2013; Nielsen et al., 2013) and higher reproductive success rates (Zedrosser et al., 2011). Forest management, particularly harvesting (i.e., logging) and silviculture regimes (i.e., post-harvest activities), affect long-term dynamics of wildlife habitat and therefore it is critical to understand how forestry activities are influencing habitat selection patterns of threatened megafauna like the grizzly bear.

The majority of foods for grizzly bear populations inhabiting interior mountains are highly concentrated in specific habitat types – predominantly early-seral forests regenerating after recent disturbance and natural openings in mature forests (Larsen et al., 2019; Munro et al., 2006). Forests in the early stages of regeneration tend to be associated with increased bear food resources and selection by interior grizzly bears (Berland et al., 2008; Nielsen et al., 2010, 2004b; Stewart et al., 2012), making them particularly important habitats. Conversely, homogenous undisturbed forest habitats have been shown to contain fewer bear foods (Nielsen et al., 2004a; Zager et al., 1983), resulting in avoidance by grizzly bears (Pigeon et al., 2016; Wielgus and Vernier, 2003).

Historically, forest regeneration in North America occurred naturally after frequent and unmanaged disturbances such as wildfire (natural and human-caused), avalanches and pest and disease outbreaks. However, more recently, anthropogenic influences have substantially altered the forest disturbance and regeneration regime across grizzly bear ranges, in turn leading to a shift in forest landscape structure. Two of the most widespread anthropogenic drivers of forest change are the suppression of wildfires and tree harvesting, often in conjunction with tree replanting. Fire suppression over the last century, primarily in commercial forests, has led to a decrease in the areal extent of shrubland and early successional forests and an increase in closed canopy and relatively homogenous forest stands (Drever et al., 2006). Forest harvesting is now the dominant cause of forest disturbance in many interior mountain regions of North America (Chavardès et al., 2018; Stewart et al., 2012) and a large portion of North American grizzly bear range is under management for timber harvesting (Nielsen et al., 2004a).

Grizzly bears are often found utilizing disturbed habitat created by forest harvesting (Nielsen et al., 2004a; Stewart et al., 2013), however it remains unclear to what degree post-harvest regenerating forests are analogous to naturally regenerating and undisturbed forests in their provisioning of resources, especially over decadal time scales. While it has been shown that initial bear food supply in regenerating forests post-harvest can be high (Larsen et al., 2019; Nielsen et al., 2004b), habitat quality may deteriorate rapidly as planted and managed forests quickly move through early seral stages. Modern forest management policies dictate that, following harvest, the nature and predicted success of regeneration must be assessed (Natural Resources Canada, 2018). If natural regeneration is judged to be sufficient, additional intervention is typically not required. Alternately, for sites with less successful natural regeneration or to meet particular management objectives, silvicultural treatments can be prescribed. Such treatments in North America often seek to maximize the re-growth of merchantable tree species through site preparation, tree planting, fertilization and herbicide application. While rapid conifer re-growth may offer certain economic incentives (e.g., sustained logging activity) and ecological benefits (e.g., carbon storage), it could pose negative outcomes for grizzly bears if the time window of early-seral habitat availability is diminished.

Studies evaluating grizzly bear selection of post-harvest regenerating forests in different geographic regions have had varied results, showing avoidance (McLellan and Hovey, 2001; Zager et al., 1983), neutral response (Berland et al., 2008; Wielgus and Vernier, 2003) and selection (Nielsen et al., 2004a; Stewart et al., 2013) of harvested forests by grizzly bears. It has been suggested that discrepancies in grizzly bear selection or avoidance of harvested areas may be linked to the availability of natural openings and disturbances. For

example, Nielsen et al. (2004a) proposed that in their study area – the foothills of the Rocky Mountains in west-central Alberta – grizzly bears were selecting for harvested areas due, in part, to a lack of natural forest openings after decades of fire suppression. Conversely, studies finding that grizzly bears avoided harvested areas tended to be in regions with abundant natural openings (McLellan and Hovey, 2001; Zager et al., 1983). However, to date, no study has been conducted over an appropriate time frame and spatial extent to empirically test the relationship between the selection of harvested areas by grizzly bears and the availability of naturally disturbed areas.

The recent production of an annual Landsat satellite time series dating back to 1984 and covering all of Canada (Hermosilla et al., 2016) allows us to accurately characterize forest disturbance and recovery over very large areas using spectral analysis (White et al., 2017). Spectrally derived forest recovery metrics, while not necessarily equivalent to structural or functional measures of recovery, have been shown to be strongly related to forest recovery benchmarks, such as canopy cover and height (White et al., 2018), but have yet to be applied to wildlife habitat selection studies. Moreover, large-area, spatially-explicit characterizations of both disturbance and recovery provide a more holistic assessment of forest dynamics (White et al., 2017).

In this study, we analyzed grizzly bear habitat selection in a region with widespread forest disturbance using vegetation, disturbance and recovery metrics derived from a 33-year satellite time series in conjunction with over 415,000 Global Positioning System (GPS) telemetry locations from 160 individual radio-collared grizzly bears collected over 18 years (295 individual ‘bear-years’) across a large area in western Alberta, Canada. Specifically, we evaluated (1) if selection of recently harvested areas was contingent upon the availability of natural disturbances, (2) how habitat selection within disturbed areas varied across disturbance types and (3) how habitat selection has changed during the first 30 years of forest recovery following different disturbance types. We focused on comparing changes in habitat selection after three main types of forest disturbance – harvesting, wildfire, and non-stand replacing disturbances – with the objective of evaluating how habitat selection changes following each disturbance type.

2. Material and methods

2.1. Study area

We conducted this study within an 118,000-km² region in the Rocky Mountains and foothills of west-central Alberta, Canada (Fig. 1). Seven provincial Bear Management Areas (BMAs) have been created across the grizzly bear range in Alberta to help manage population recovery of the species, which was officially listed as ‘Threatened’ by the province in 2010 (Clark and Slocombe, 2011; Festa-Bianchet, 2010). We focused this study on four of these BMAs – Swan Hills, Grande Cache, Yellowhead and Clearwater – due to their large number of collared bears, and the mosaic of regenerating forests following recent disturbances within them. Together these four BMAs account for 68% of the total provincial BMA coverage.

The climate is continental, with very short cool summers at high elevations and short warm summers in the foothills (Natural Regions Committee, 2006). The highest elevations are primarily rock and permanent snow and ice, with alpine meadows and open subalpine forests near treeline. At lower elevations, a mosaic of forest types and ages exists, largely influenced by disturbance. Before the implementation of widespread fire suppression in the early 1900s, the primary disturbance regime was characterized by periodic stand-replacing fires (Anderson, 1998; Chavardès et al., 2018; Rhemtulla, 1999). In the 20th century, natural disturbances became more sporadic, limited primarily to isolated high-intensity fires and non-stand replacing disturbances, likely linked to forest maturation (Thorpe and Daniels, 2012), drought stress (Peng et al., 2011) and insect damage, such as the recent expansion of mountain pine beetle (Safrañyik et al., 2010). This led to an expansion of closed-canopy conifer forests (primarily lodgepole pine *Pinus*

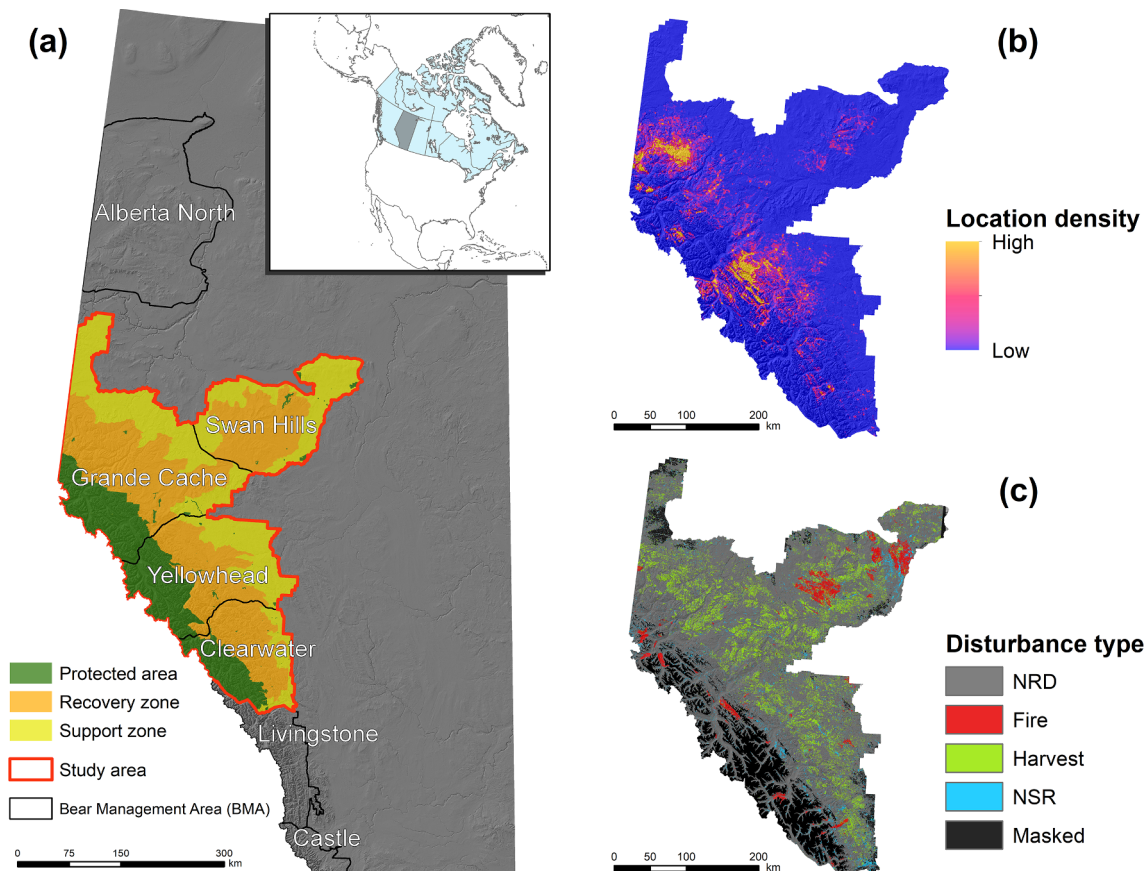


Fig. 1. Maps of the study area in western Alberta, Canada. Panel (a) shows the seven provincial Bear Management Areas (BMAs), the four BMA's that make up the study area, protected areas and grizzly bear recovery and support conservation zones (see Nielsen et al., 2009). Panel (b) shows the location density of all GPS telemetry observations used in the seasonal RSF models (i.e., used locations) and panel (c) shows areas not recently disturbed (NRD), the three most common forest disturbance types – fire, harvest and non-stand-replacing (NSR) – and the areas masked from analysis (elevations > 2100 m and agricultural land uses; see Methods).

contorta, spruce *Picea* spp. and fir *Abies* spp.) and a reduction in shrub and broadleaf cover. Industrial logging activity began in the 1950s (Andison, 1998) and expanded rapidly in the foothills outside of protected areas beginning in the 1980s (White et al., 2011) creating temporary openings of young stands, typically followed by planted conifer trees. Oil and gas development in the region began around the same time as industrial logging and increased substantially after 2000 (Pickell et al., 2015).

Early seral-stage forests and natural openings in the study area tend to contain numerous bear foods in the form of annual forbs (e.g., *Heracleum lanatum*), grasses, roots (e.g., *Hedysarum* spp.) and berry-producing shrubs (e.g., *Vaccinium* spp.) (Munro et al., 2006). The region supports a wide range of potential prey, but ungulates and, to a lesser extent insects and rodents, tend to be the primary animal food sources for grizzly bears (Munro et al., 2006).

2.2. Telemetry data and home range estimation

We modeled grizzly bear habitat selection at the population level with resource selection functions (RSFs) derived from environmental co-variates extracted at used and available locations within bears' seasonal home ranges (third-order selection; Johnson, 1980). Used locations corresponded to known GPS telemetry fixes from captured and radio collared grizzly bears, whereas available locations corresponded to randomly selected locations within the seasonal home range of each individual grizzly bear. Grizzly bears were collared by fRI Research (Hinton, Alberta) from 1999 to 2016 using leg snaring, aerial darting and culvert traps. Capturing methods were approved annually by the University of Saskatchewan Animal Care Committee and by the Alberta

Environment and Sustainable Resource Development and followed Canadian Council of Animal Care protocols (Animal use Protocol Number 20010016). Bears were fitted with one of three collar types – Advance Telemetry Systems (ATS, Isanti, MN, USA), Televilt (Televilt, Lindesberg, Sweden) or Followit (formerly Televit) – programmed to transmit locations at intervals ranging from < 30 min to up to 4 h.

We separated telemetry data into three seasons prior to home range estimation and modeling to account for seasonal variation in food habits and habitat selection (Berland et al., 2008; Munro et al., 2006; Nielsen et al., 2004a). The seasons represent approximately two-month intervals, defined as follows: Hypophagia – den emergence (typically mid-April) to 15 June; Mesophagia – den emergence (typically mid-April) to 15 June; Mesophagia – 16 June to 15 August; Hyperphagia – 16 August to 15 October. During Hypophagia, bears tend to feed on roots and ungulates. During Mesophagia (also called early-Hyperphagia), food intake increases and foraging broadens to include insects, graminoids, forbs and some early season berries. During Hyperphagia (also called late-Hyperphagia), frugivory generally increases until mid-September, at which point late digging of roots again increases (Munro et al., 2006).

We calculated home ranges using telemetry locations resampled to six hour intervals to avoid bias and achieve regularly spaced observations across all individuals (Fieberg, 2007). For each season, we removed from the dataset any bears with fewer than 60 observations, or with observations covering fewer than 30 days. To develop individual seasonal home ranges we calculated the 95% kernel density of used locations within each season for each unique bear-year, and buffered this by the 95th percentile of observed daily travel distances, calculated for each age-sex class. We then resampled the original dataset to a minimum fix rate of one hour and generated five random available

Table 1

Model input variables and descriptions. Ranges for *Terrain* and *Vegetation* variables reflect values observed in used (GPS telemetry) and available (randomly generated within home ranges) locations across all bears. Ranges for *Disturbance* variables are only relevant for used and available locations with detected disturbances, except disturbance type which is categorical with four classes: not recently disturbed, harvest, fire, non-stand replacing. Range values with an asterisk (*) were manually truncated (see Methods).

| Description | Units | Median (Range) |
|---|------------------------------------|--|
| <i>Terrain</i> | | |
| Elevation | meters | 1360 (497–2099 [*]) |
| Insolation/solar radiation | watt hours $m^{-2} \times 10^5$ | 9.9 (6.8–13.1) |
| Topographic wetness | index | 8.13 (6.13–12.51) |
| <i>Vegetation</i> | | |
| Normalized burn ratio (NBR) ^a | index | 0.60 (–0.87 to 0.99) |
| Tasseled cap greenness (GRN) ^a | index | 864 (–1984 [*] to 4636) |
| Distance to forest edge ^a | meters | –60 (–2817 to 4943) |
| <i>Disturbance</i> | | |
| Disturbance type | class | See caption |
| Time since disturbance ^a | years | 10 (0–30) |
| Disturbance intensity | Δ NBR | –0.49 (–1.85 to 0.00 [*]) |
| Spectral recovery of NBR ^a | % | 80 (0 [*] –200 [*]) |
| Pre-disturbance NBR | index | 0.62 (0.00 [*] –1.00) |
| Pre-disturbance GRN | index | 710 (–2000 [*] to 4809) |

^a Variables computed annually.

locations for every used location within each home range (Koper and Manseau, 2012). We did not remove locations with high positional dilution of precision from the analyses to avoid potential bias toward open terrain and vegetation (Ironside et al., 2017). After preprocessing and cleaning (see below) of the one-hour interval telemetry data used for analyzing habitat selection, seasonal observations included 144 bear-years and 97,601 used GPS locations during Hypophagia, 237 bear-years and 176,674 locations during Mesophagia and 199 bear-years and 141,524 used locations during Hyperphagia.

2.3. Satellite-derived habitat covariates

We created habitat covariates representing terrain, vegetation conditions, disturbance and recovery using satellite imagery at 30 m spatial resolution (Table 1). We chose terrain and vegetation variables that represent natural habitat features shown to be related to food availability (e.g., Nielsen et al., 2010) and habitat selection (e.g., Nielsen et al., 2009). Disturbance variables represented the type and intensity of disturbance, and recovery represents the regeneration of forest vegetation (i.e., trees).

We derived three terrain covariates from a void-filled digital elevation model produced from the NASA Shuttle Radar Topography Mission: elevation in meters, solar insolation and a topographic wetness index. We calculated insolation in ArcGIS v10.5 (ESRI, 2017) and it gives an estimate of the integrated annual solar energy that reaches the earth, accounting for variation in slope, aspect and shadows. The topographic wetness index (TWI) represents surface water flows and accumulation and we calculated it as:

$$TWI = \ln\left(\frac{f}{\tan s}\right) \quad (1)$$

where f is the upslope contributing area in meters and s is slope in radians of a given pixel. In order to remove extreme values and better capture riparian zones, we smoothed the final index using a 300 m radius circular moving window.

We derived vegetation, disturbance and recovery covariates from a time series of best-available-pixel composites of surface reflectance from annual Landsat images (TM, ETM+ and OLI sensors) produced for

Canada (Hermosilla et al., 2016). The Landsat composites were created by analyzing the available time series (1984–2016), choosing the best pixel based on data quality, and infilling with temporally smoothed proxy values to create a gap-free annual surface reflectance composite (see Hermosilla et al., 2015a for a complete description). Surface reflectance values were then multiplied by 10,000 and converted to integer format for storage and processing efficiency. Disturbances were detected using breakpoint analysis and attributed to a change type using a Random Forest classifier applied to the same 1984–2016 time series of Landsat composites (Hermosilla et al., 2015b). We calculated time since disturbance in years and separated disturbance change types into four classes: not recently disturbed (i.e., since 1984), harvest, fire and non-stand replacing. Non-stand replacing disturbances were defined as areas of low magnitude forest change associated with biotic (e.g., insect) and abiotic (e.g., flooding) events that did not result a change in land cover class (Hermosilla et al., 2015b). Disturbances considered more permanent (e.g., agriculture, roads, oil and gas well sites) were detected in the area, but were not included in this study since we were primarily focused on analyzing regenerating forest and not recently disturbed locations. We also masked all locations above 2100 m (approximate tree line) and those identified as permanent snow/ice or water (see Fig. 1).

From the Landsat composites, we produced annually two vegetation indices: the normalized burn ratio (NBR) and tasseled cap greenness (GRN). NBR has been shown to be correlated with forest structure variables such as canopy height and closure (Pascual et al., 2010), and is related to stand age and complexity (Key and Benson, 2006; Pickell et al., 2016). GRN has been shown to be strongly related to vegetation cover and vigor (Crist and Ciccone, 1984; Liu et al., 2016), but poorly correlated with forest structure variables (Cohen and Spies, 1992), and thus is related to herbaceous ground cover and understory. Therefore, different possible combinations of these two indices were expected to represent a wide range of habitat conditions. We calculated NBR as:

$$NBR = \frac{NIR - SWIR}{NIR + SWIR} \quad (2)$$

where NIR is the near infrared band and SWIR is the shortwave infrared band, yielding possible values between –1 and 1. We calculated GRN using coefficients developed by Liu et al. (2016).

We quantified disturbance intensity by taking the difference in NBR between the year prior to the disturbance event and the year the disturbance was detected. To estimate forest recovery for each year following disturbance, we created a ‘spectral recovery’ metric calculated as the NBR value for that year divided by the average NBR value in the two years prior to disturbance. Spectral recovery can serve as a useful proxy for vegetation recovery following stand-replacing disturbance (Frolking et al., 2009; Griffiths et al., 2014). Previous research has confirmed the utility of NBR-derived spectral recovery values for characterizing the return of forest structure (White et al. 2018), with a threshold of 80% of pre-disturbance NBR commonly used to indicate when a forest has ‘recovered’ to benchmark levels of canopy cover (> 10%) and height (> 5 m) following a stand-replacing disturbance (Bartels et al., 2016; Pickell et al., 2016; White et al., 2018, 2017). We also extracted average pre-disturbance GRN and NBR values using the mean of each respective index for the two years before disturbance.

We identified forest edges for each year from annual land cover maps created by Hermosilla et al. (2018) from the same Landsat composites used to create the vegetation indices. We defined forest edges as any cell with at least three neighboring cells classified as forest and at least three classified as non-forest in a moving window of 3×3 cells (900 m²).

We cleaned the dataset prior to modeling to remove outliers and possible errors (see Table 1). Specifically, we removed GRN values less than –2000 after visual inspection showed these represented a small number of non-vegetated pixels not captured by our mask. From locations with detected disturbances, we removed pre-disturbance GRN values less than –2000 and pre-disturbance NBR values less than 0.0, as these values were detected as outliers and also unlikely to have been

forested prior to disturbance. We truncated spectral recovery values at 0% and 200% in order to eliminate negative recovery values and remove a limited number of extreme values that resulted from dividing by a low initial NBR.

2.4. Grizzly bear selection of harvested areas

Our first objective was to test whether selection of recently harvested areas changed depending on the availability of natural disturbances (i.e., fire and non-stand replacing) within a grizzly bear's home range. To do this, we calculated the proportional area of natural disturbances relative to harvested area within the observed home range for each year and separated individual bear-years into two groups based on natural disturbance availability: (1) limited – a ratio of less than 0.5, (2) abundant – a ratio of greater than 0.75. We then developed separate logistic regression models for the two groups for each season and for daytime, nighttime and crepuscular (i.e., dawn/dusk) periods. We included a three-class categorical independent variable of disturbance type (not recently disturbed, harvest, natural) and a binary dependent variable of used (1) and available (0) locations. We calculated odds ratios and their 95% confidence intervals using a cluster-robust covariance matrix (Cameron et al., 2011) with individual bear-year defined as the cluster variable to account for correlation within individual bears. The not recently disturbed class was set as the reference category. In this manner, if the odds ratio is 1.0, locations are being used as available, and neither selection nor avoidance is said to be occurring. If values are greater than 1.0, we consider locations to be selected relative to not recently disturbed locations, while values less than 1.0 indicate relative avoidance. When confidence intervals are overlapping 1.0, neither selection nor avoidance can be concluded with statistical significance.

2.5. Modeling habitat selection within disturbed areas

Our second objective was to evaluate how habitat selection differed between disturbance types. To do this, we created separate seasonal RSFs for not recently disturbed locations and for locations in each of the three disturbance types (harvest, fire, non-stand replacing). We then fit generalized linear mixed effects logistic regression models, with a random intercept specified as individual bear-year nested within reproductive class, and fixed effects specified from the satellite-derived co-variables (Table 1). The random intercept allows for differing response magnitudes to habitat covariates by individual bears and by reproductive class groups, both of which have been commonly observed in previous grizzly habitat selection studies (e.g., Nielsen et al., 2004a; Stewart et al., 2013). We fit models using the *glmer* function in the *lme4* package (Bates et al., 2015) in R v3.4.1 (R Core Team, 2016).

For disturbed locations, we built RSF models using the entire suite of variables from Table 1, whereas for not recently disturbed locations, we built models using only the terrain and vegetation variables. We input all continuous variables as second order polynomials due to demonstrated nonlinear relationships between terrain variables and grizzly bear foods and habitat selection (Nielsen et al., 2010; Roever et al., 2008), and hypothesized nonlinear responses to vegetation structure/greenness and disturbance intensity. We specified fixed effects interactions between: each of the terrain variables and each of the two vegetation indices (pre- and post-disturbance); the two vegetation indices themselves; NBR and the disturbance metrics; disturbance type and each of the two vegetation indices, distance to edge and the disturbance metrics.

In order to determine whether disturbance-specific models and the satellite-derived disturbance metrics improved predictive performance across the population, we extracted validation measures from the fully specified seasonal RSF models and compared them to base RSF models that were fit to the entire dataset for each season using only the terrain and vegetation variables.

We developed validation measures using bootstrapped cross-validation on withheld individuals. For each bootstrap iteration, we

randomly withheld 20% of the individuals from each reproductive class and built each model on the remaining dataset, repeating this process 101 times. In this manner, all individuals were weighted equally during validation regardless of the number of GPS locations available for each individual. This method is considered more robust for population-level presence/absence predictions and less prone to bias from data-rich individuals compared to withholding a percentage of pooled data across all individuals (Koper and Manseau, 2012).

During each iteration, we created ten bins from the predicted probability of use cut at (from lowest to highest): the 10th, 20th, 30th and 40th percentiles of available locations, the overall median, and the 60th, 70th, 80th and 90th percentiles of used locations. We created the ten probability bins in order to extract validation measures based on the area-adjusted frequency of used locations within each probability bin. We calculated area-adjusted frequency following methods developed by Boyce et al. (2002). In short, it is the frequency of used locations within each probability bin, adjusted for unit area. It was calculated as the frequency of used locations within each bin, divided by the available area with a predicted RSF within that bin for each bootstrapped iteration. We then log transformed the area-adjusted frequency value, whereby a value of zero indicated that used locations occur at random relative to available locations, positive values indicated used locations occurred more frequently than random, and negative values less frequently. We expect a model with good predictive performance to show a positive correlation in area-adjusted frequency (more used locations in higher probability bins), have minimal variation across individuals, and always be different from zero since the bottom five bins were designed to indicate avoidance and the top five bins to indicate selection. To this end, we produced three validation measures: (1) the Spearman rank correlation between area-adjusted frequency and bin, (2) the within-bin variance of area-adjusted frequency and (3) the proportion of bins significantly different from zero. For the third validation statistic, we ran one-tailed t-tests to evaluate if the bottom five bins were significantly less than zero and if the top five bins were greater than zero, respectively. While validation measures were calculated on ten bins, we deemed six bins (cut at the 20th, 40th, 50th, 60th, and 80th percentiles described above) to be an effective number and used this for visualization purposes.

We examined the average effect of individual disturbance metrics on predicted probability of use (Avgar et al., 2017) for RSF models built for areas with recent disturbance. For this, we plotted predicted probability of use for available locations across the observed range of the metric of interest, and then fit a generalized additive model with a cubic regression spline smooth term to the data using the *stat_smooth* function in R v3.4.1 (R Core Team, 2016). We focused this analysis on vegetation and recovery metrics derived from the satellite time series.

2.6. Change in habitat use over time

Our final objective was to characterize how habitat selection has varied over time. To analyze decadal effects of forest regeneration on grizzly habitat use after different disturbance types, we compared predicted probability of use for up to 30 years following recent disturbance. We predicted probability of use pre- and post-disturbance across the study area for each of the three seasons using the seasonal RSF models and categorized the predicted probability into six bins, as described above. We also plotted the change in NBR and distance to forest edge for each disturbance type to explore how forest structure changed during regeneration, and how this relates to RSF predictions.

3. Results

3.1. Grizzly bear selection of harvested areas

The odds of selecting harvested areas varied by season and abundance of natural disturbances (Fig. 2), but not by time of day (results not shown). When the availability of naturally disturbed areas was

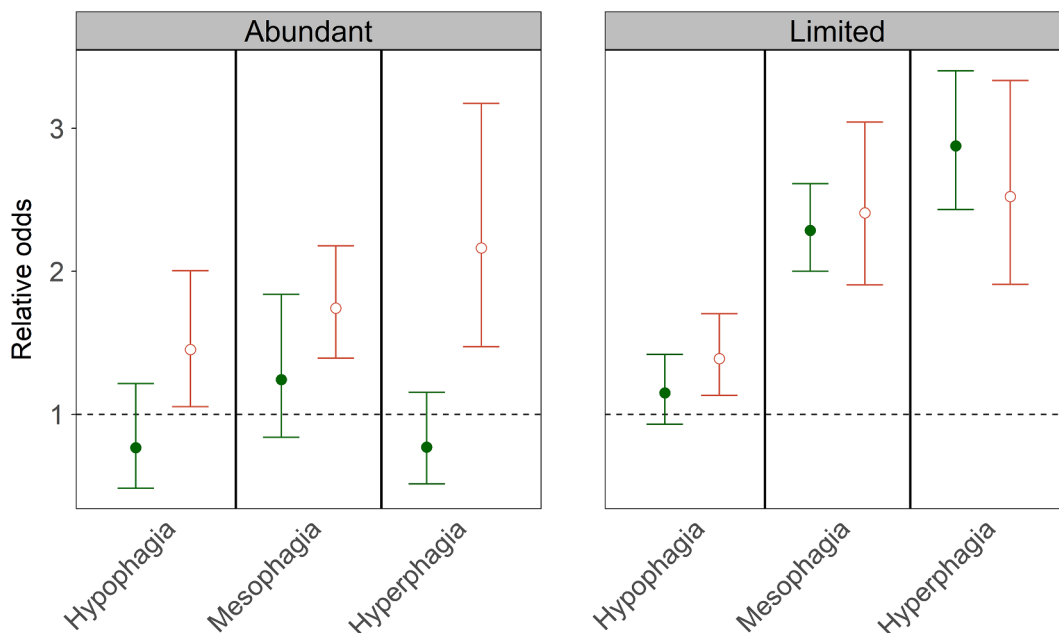


Fig. 2. Odds of selection for harvested (filled circle) and natural disturbances (open circle) relative to not recently disturbed locations. Odds less than one (horizontal dashed line) indicate avoidance and odds greater than one indicate selection. Availability of natural disturbances – wildfire and non-stand replacing disturbances – is the ratio of the available area of these disturbances relative to the available area of harvesting disturbances, where Abundant (left) is a ratio of at least 0.75 and Limited (right) is a ratio of less than 0.5. Error bars indicate the 95% confidence interval calculated from robust standard errors.

abundant, relative selection of harvested areas was slightly less than expected based on availability (i.e., less than one) during Hypophagia (0.77) and Hyperphagia (0.77), and slightly more than expected during Mesophagia (1.24). However, differences in selection were not different from neutral (value = 1.0) for any season at the 95% confidence level (Fig. 2). When the availability of natural disturbances was limited, the odds of selection for harvested areas was significantly higher than expected based on availability during Mesophagia and Hyperphagia. The relative odds of selection of natural disturbances was always significantly greater than one irrespective of season and availability.

3.2. Habitat selection within disturbed areas

Seasonal RSF models built for disturbed locations improved the majority of validation measures compared to seasonal base models, whereas for not recently disturbed locations they were equivalent (Table 2). Improvement in correlation between probability bins and area-adjusted frequency was greatest for harvested areas and non-stand replacing disturbances, whereas correlation decreased for fire. However, overall the probability bins were correlated with area-adjusted frequency of occurrence across all disturbances (Fig. 3; Table 2), confirming that the models do have reasonable predictive power for new individuals.

Looking at the effects of individual input variables, across all areas, predicted probability of use by grizzly bears tended to be higher at higher levels of GRN (> 900) and intermediate values of NBR (0.3–0.6), with a strong interaction between the two indices (Fig. 4a). Locations with high GRN and intermediate NBR likely represent areas with high vegetative cover, but low canopy height and closure. At NBR values above ~0.7 (indicative of older, denser forest stands with higher canopy closure), probability of use was low, irrespective of GRN values. Distance to forest edge was also a strong predictor and in general grizzly bears selected against locations inside forests and for locations near, but outside, the forest edge. In disturbed areas, probability of use was highest < 350 m outside the forest edge (Fig. 4b).

Table 2

Validation measures for seasonal base models and fully specified models built for each disturbance type. Validation measures were computed from bootstrapped cross-validation (101 iterations), withholding 20% of individual bears, stratified by age-sex-reproductive class. ‘Correlation’ is the average Spearman rank correlation coefficient between area-adjusted frequency of occurrence and the ten probability bins created from each RSF model. ‘Variance’ is the within-bin variance of area-adjusted frequency of occurrence across all iterations. ‘Proportion ≠ 0’ is the proportion of bins with an area-adjusted frequency that is significantly different from zero based on one-tailed t-tests ($p < 0.05$).

| Disturbance type | Model | Correlation | Variance | Proportion ≠ 0 |
|------------------------|-------|-------------|----------|----------------|
| <i>Hypophagia</i> | | | | |
| Not recently disturbed | Base | 0.99 | 0.004 | 1.0 |
| | Full | 0.99 | 0.005 | 1.0 |
| Harvest | Base | 0.73 | 0.244 | 0.7 |
| | Full | 0.87 | 0.017 | 1.0 |
| Fire | Base | 0.90 | 0.374 | 0.7 |
| | Full | 0.81 | 0.162 | 1.0 |
| Non-stand replacing | Base | 0.88 | 0.111 | 0.8 |
| | Full | 0.94 | 0.028 | 1.0 |
| <i>Mesophagia</i> | | | | |
| Not recently disturbed | Base | 0.99 | 0.003 | 1.0 |
| | Full | 0.99 | 0.003 | 1.0 |
| Harvest | Base | 0.98 | 0.100 | 0.9 |
| | Full | 0.94 | 0.007 | 1.0 |
| Fire | Base | 0.96 | 0.122 | 0.8 |
| | Full | 0.89 | 0.060 | 1.0 |
| Non-stand replacing | Base | 0.98 | 0.078 | 0.9 |
| | Full | 0.98 | 0.012 | 1.0 |
| <i>Hyperphagia</i> | | | | |
| Not recently disturbed | Base | 0.98 | 0.008 | 1.0 |
| | Full | 0.98 | 0.010 | 1.0 |
| Harvest | Base | 0.75 | 0.247 | 0.8 |
| | Full | 0.90 | 0.014 | 1.0 |
| Fire | Base | 0.90 | 0.394 | 0.8 |
| | Full | 0.84 | 0.120 | 0.9 |
| Non-stand replacing | Base | 0.89 | 0.114 | 0.8 |
| | Full | 0.95 | 0.022 | 1.0 |

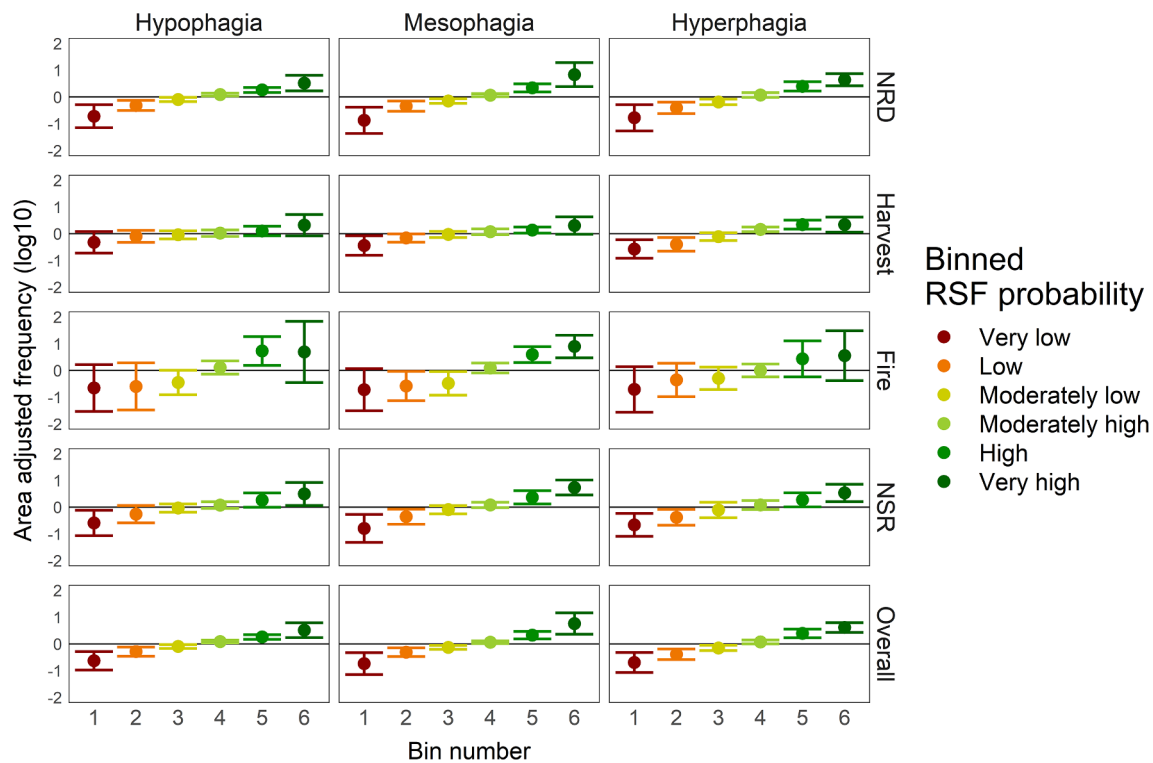


Fig. 3. Probability of use predicted by the resource selection function (RSF) grouped into six bins (reduced from the original ten bins to improve readability) and plotted against the log of the area adjusted frequency of occurrence for each season (columns) and each disturbance type (rows; NRD = not recently disturbed, NSR = non-stand replacing). Log-transformed frequency values less than zero (horizontal lines) indicate occurrence less often than expected at random and values greater than zero indicate occurrence more often than expected at random.

Spectral recovery and time since disturbance were strong predictors of use in harvested areas (Fig. 5). Spectral recovery tended to increase with time since disturbance, however the two variables were only moderately correlated across disturbance types (Pearson's r : Harvest = 0.62; Fire = 0.43; non-stand replacing = 0.27). As time since disturbance increased in harvested areas, grizzly bears selected for locations with the least spectral recovery, and tended to select against areas harvested more than 20 years prior, especially during Mesophagia and Hyperphagia. After fires, selection was more strongly tied to time since disturbance than spectral recovery, and grizzly bears tended to select for locations burned at least 8–10 years ago, irrespective of spectral recovery, except during Hyperphagia when they selected against very low recovery (< 40%). In non-stand replacing disturbances, there was some selection for younger disturbances (< 10 yrs.) with lower spectral recovery (< 60%) during Hyperphagia, but in general time since disturbance and spectral recovery were not strong predictors of use.

The effect of disturbance intensity on selection probability varied by season and disturbance type, although overall trends were weak (data not shown). Fires typically had the highest intensity (average NBR change magnitude = -0.71), followed by harvest (-0.48) and non-stand replacing (-0.29). Generally, grizzly bears selected for harvested locations with lower disturbance intensity. They selected for lower intensity fires in Hypophagia and higher intensity fires in Hyperphagia, while Mesophagia selection was neutral. Among non-stand replacing disturbances, selection was strongest for higher intensity disturbances.

3.3. Change in habitat selection over time

Prior to disturbance, the distribution of probability bins was similar in areas disturbed by harvesting and fire, and approximately 20–30% of area was in the upper three bins (“Moderately high”, “High”, and “Very high”) for both disturbance types in all seasons (Fig. 6). In areas with non-stand replacing disturbances, there was a slightly greater

proportion of area in the upper three bins (~50%).

Across the entire study area, in harvested locations during Hyperphagia, the proportional area in upper bins immediately increased, whereas during Hypophagia and Mesophagia the area initially decreased for about 2–3 years, then increased (Fig. 6). For all three seasons, after 15–20 years, the proportional area in the upper three bins was lower than prior to harvesting, and at 30 years the area in the lowest bin had increased by between 1.7 times (for Hyperphagia) and 3.0 times (for Hypophagia).

In burned locations, at 30 years, the area in the upper three bins was equal to or greater than pre-disturbance, and the area in lowest bin increased, although less than after harvesting, ranging from 1.1 times (Hyperphagia) to 2.2 times (Mesophagia). However, it is worth noting that the burned area between 20 and 30 years old was limited (average of 59 km²). After non-stand replacing disturbances, there was a delayed and steady decline, beginning after about 10 years, in the upper bins during Hypophagia and Mesophagia, and an increase of up to 3.1 times in the lowest probability bin compared to pre-disturbance. During Hyperphagia, changes were minimal over the 30-year period. An example map of change in predicted probability of use over time after harvest and fire is shown in Fig. 7 for a region within the Grande Cache BMA (see Fig. 1 for BMA location).

Temporal trends in habitat selection (i.e., distribution of probability bins) were linked, at least in part, to changes in vegetation metrics detected by satellite. In harvested locations, changes in NBR and distance to forest edge indicated that, for the majority of locations, conditions were no longer in the ‘preferred’ selection range for these two variables (see Fig. 4) after about 15–20 years (Fig. 8). This coincides with the years since disturbance at which the area in the upper three probability bins fell below pre-disturbance areas for harvested locations (Fig. 6). Additionally, in harvested areas the variance in NBR at ~20 years became very small and the majority had NBR exceeding pre-disturbance NBR values.

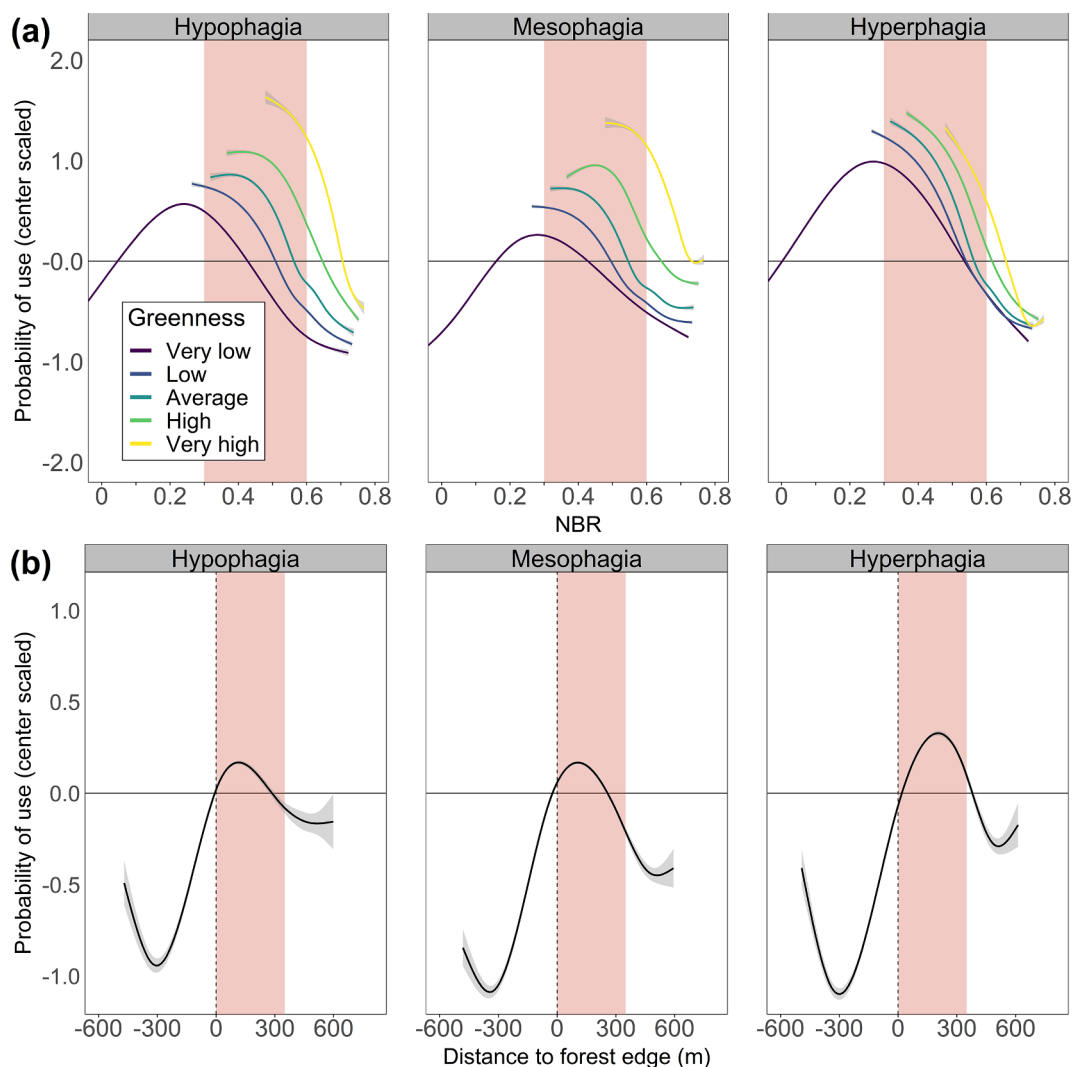


Fig. 4. Fitted smoothing curves (using generalized additive models) showing the modelled effect of (a) vegetation structure (NBR) and greenness (GRN) and (b) distance to forest edge on the probability of use by grizzly bears for the three seasons for all available locations. Negative values of distance to forest edge (b) indicate locations inside the forest and positive values outside. Probabilities were center scaled to allow multi-model plotting, and values above zero (horizontal line) indicate probabilities above the median (i.e., selection). The ranges highlighted in red correspond to manually identified ranges of high probability of use for NBR and distance to forest edge, respectively, and are included to aid in visual comparison with Fig. 8. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

In burned areas, for the first 5–10 years NBR was well below the preferred range, but then generally remained within it. Variance of NBR was high across the entire time series. Distance to edge was within the preferred range for the majority of locations across all years, and variance was higher than in harvested locations. Values for the two variables following non-stand replacing disturbances tended to be intermediate to harvesting and fire, and changes were less pronounced.

4. Discussion

4.1. Grizzly bear selection of regenerating forests following harvest

Forest disturbance creates valuable habitat for grizzly bear populations in interior mountain regions. We showed that forest harvesting provided attractive habitat when natural disturbances were scarce, as suggested by Nielsen et al. (2004a). However, when grizzly bears had the choice, they were more likely to select naturally disturbed areas compared to harvested forests within their home range (Fig. 2).

One explanation for this result could be that natural disturbances simply provide better resources (e.g., food) than harvested areas and,

when given the choice, grizzly bears will select for them. However, increased human activity due to better access (e.g., roads) in recently harvested areas is known to influence bear survival (Boulanger et al., 2014) and may also be influencing selection of harvested areas. Wielgus and Vernier (2003) found that grizzly bears in the Selkirk mountains of British Columbia were four times more likely to select for natural openings compared to cutblocks in an area where roads were open to the public, but that selection for natural and cutblock openings were similar where roads were closed. Nielsen et al. (2004a) found that grizzly bears were more likely to select for cutblocks at night, suggesting they may be avoiding humans. We compared daytime and nighttime selection of harvested forests in our study area and did not find differences between them, irrespective of the availability of natural disturbances. This suggests that human activity may not be a major factor in grizzly bear use of harvested forests, although public road access and timing of harvest relative to use may be better indicators of human activity. We did not analyze the influence of roads on selection in this study due to a lack of accurate time series data reflecting changes in road access over time. The availability of annual data on road locations, access and human activity would enable better understanding

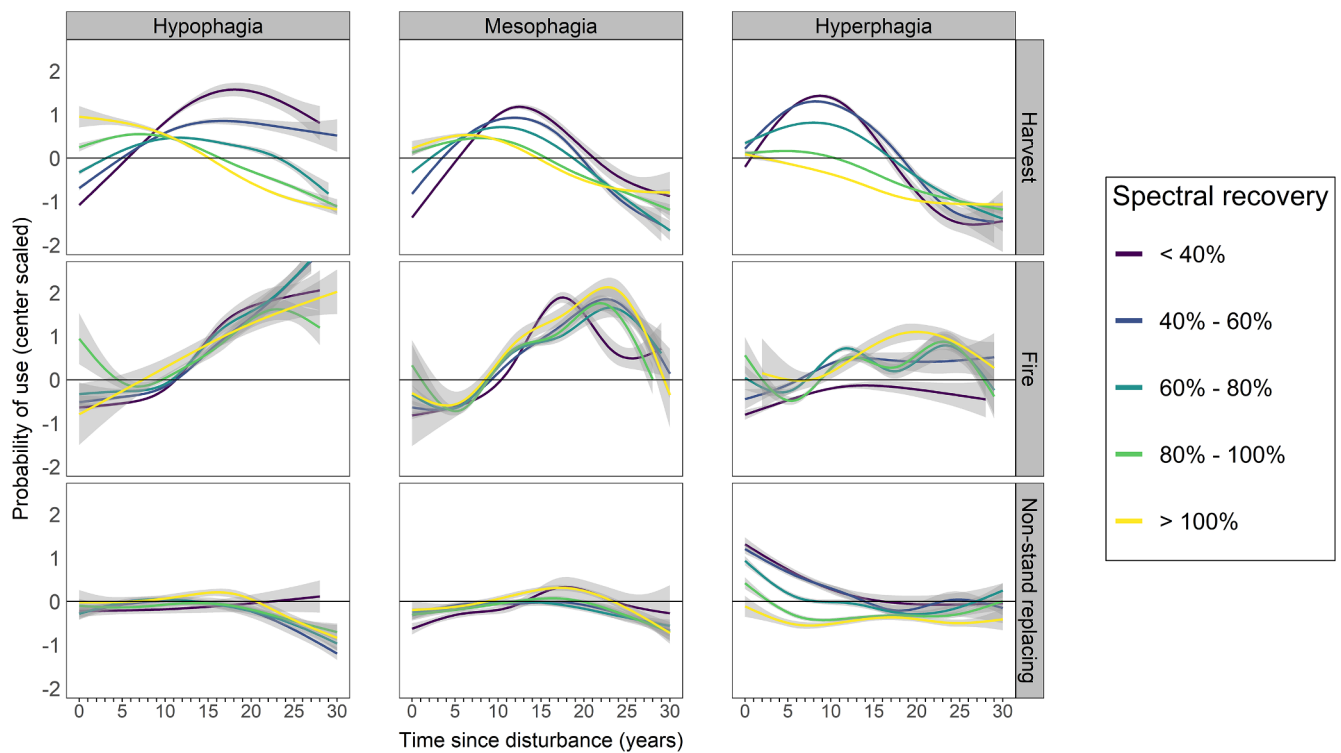


Fig. 5. Fitted smoothing curves (using generalized additive models) showing the modelled effect of time since disturbance and spectral recovery on the probability of use by grizzly bears for available harvested locations. Spectral recovery is the observed Normalized Burn Ratio (NBR) – a satellite derived vegetation index linked to forest structure – relative to the average NBR for the two years prior to disturbance. Probabilities were center scaled to allow multi-model plotting, and values above zero (horizontal line) indicate probabilities above the median (i.e., selection).

of the relative influences of risk and resource availability in grizzly bear use of harvested forests.

Our results suggest seasonal differences may exist in selection of harvested areas. In particular, forest harvesting may be reducing the attractiveness of early seral habitat relative to natural disturbances during Hyperphagia. We found a trend of increasing relative odds of selection over the course of the year (i.e., Hypophagia < Mesophagia < Hyperphagia) for natural disturbances, as well as for harvested forests when natural disturbances were limited (Fig. 2). However, the trend did not hold for harvested forests when natural disturbances were abundant. Instead, the odds of selection decreased during Hyperphagia and was significantly lower than for natural disturbances (Fig. 2). These results align well with the study by Nielsen et al. (2004a), where they found no selection of cutblocks during Hypophagia, positive selection during Mesophagia and avoidance during Hyperphagia.

These findings may be related to how harvesting promotes or reduces different bear foods. Grizzly bear consumption of grasses, forbs and insects peaks during Mesophagia (Munro et al., 2006), and it has been shown that the presence of ants, grasses and some forbs (both endemic and exotic) may occur at higher frequencies in cutblocks compared with reference forest stands (Larsen et al., 2019; Nielsen et al., 2004b; Zager et al., 1983). During Hyperphagia, berries become the principal food source until no longer available, at which point grizzly bears turn to digging roots (Munro et al., 2006). Several berry species important for grizzly bears (e.g., *Vaccinium* spp.) have been found to be negatively associated with harvesting, except near the forest edge (Larsen et al., 2019; Nielsen et al., 2004b; Zager et al., 1983). Furthermore, soil-disturbing site management practices have been shown to have adverse effects on the presence of roots and some berries, whereas forbs and grasses respond positively to soil disturbance (Haeussler et al., 1999; Moola and Mallik, 1998; Nielsen et al., 2004b). By contrast, many berry producing shrubs thrive where fires return often (every 25–60 years) and intensity is low, peaking around 20–30 years after disturbance (Tirmenstein, 1990). Shrubs surviving under closed canopies but with

reduced berry production (Zager et al., 1983) would also likely benefit from increased light penetration and understory growing conditions following non-stand replacing disturbances.

It remains less clear how the abundance and distribution of important ungulate species as prey for grizzly bears are related to forest harvesting in this area. The removal of overstory during forest harvesting can increase browse resources for key prey species such as moose, deer and, to a lesser extent, elk (Potvin et al., 2005; Stelfox et al., 1976; Strong and Gates, 2006). However, mechanical disturbance and herbicide spraying can decrease browse biomass for up to 20 years relative to unharvested forests, especially during winter (Milner et al., 2013; Strong and Gates, 2006), and moose have been shown to avoid sprayed stands in Norway (Milner et al., 2013). Furthermore, ungulates tend to avoid open areas due to perceived risk from hunters and predators, as well as deeper winter snow pack which inhibits movement (Courtois et al., 2002; Tømm et al., 1981). Older studies within our study area showed that, in general, ungulate presence was lower than expected within harvests and below carrying capacity (Stelfox et al., 1976), though deer frequently used harvest peripheries and moose tolerated recent harvests as long as nearby human activity was low (Tømm et al., 1981). Meanwhile, ungulate consumption by grizzly bears was found to primarily occur close to forest edges within moderate and dense conifer areas with high vegetation cover (Cristescu et al., 2014). The overall relationship between forest harvesting and ungulate distribution is likely scale dependent (Courtois et al., 2002; Cristescu et al., 2014) and closely related to prevailing silviculture practices.

4.2. Change in habitat use over time

The average window of time for which harvesting provides attractive habitat appears to be limited to about 20 years for all seasons and, by the end of the 30-year period, there was a substantial decrease in the amount of highly attractive habitat compared to pre-disturbance (Fig. 6). These results differ somewhat from the only other study of grizzly bear use of harvested locations by time since disturbance for this

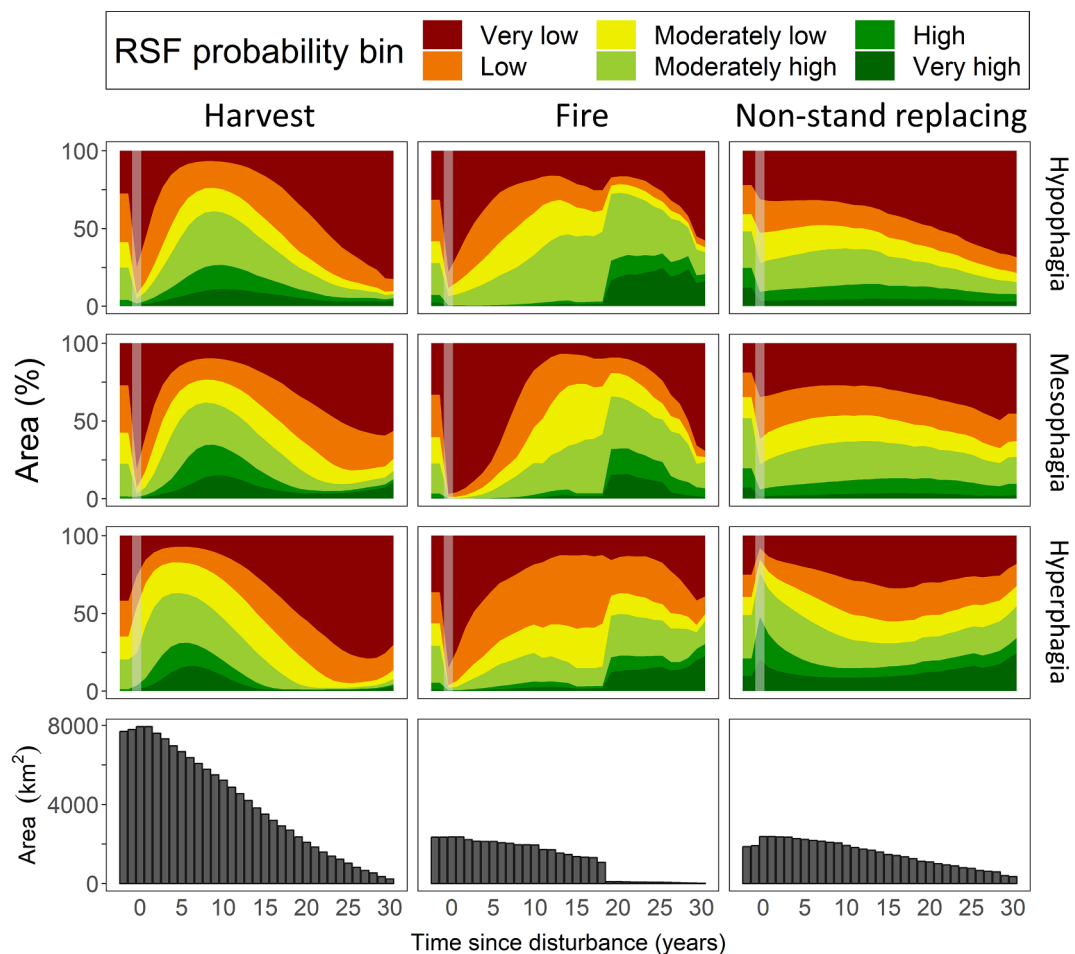


Fig. 6. Modelled change in binned probability of use following disturbance across the study area. The top three rows show the proportional area in each resource selection function (RSF) probability bin for two years prior and up to 30 years after all detected disturbance in the study area. The white vertical bar highlights year zero, when the disturbance was detected. Histograms (bottom row) show the area of each disturbance observed for each time period.

region, where [Nielsen et al. \(2004a\)](#) found that the probability of use was highest for cutblocks aged 20–40 years during Hypophagia and greater than 35 years during Hyperphagia. There are several possible explanations for this discrepancy. First, our study did not account for harvested areas greater than 30 years old due to a lack of consistent satellite imagery prior to 1984. There could be an increase in selection as harvested stands continue to regenerate beyond 30 years; although this seems unlikely given the observed response to recovery-related variables. Second, the study by [Nielsen et al. \(2004a\)](#) did not include temporally explicit variables related to forest regeneration, nor account for spatial variation of recovery within cutblocks. Our study showed that the level of spectral recovery influenced the time since disturbance of harvest location selected by grizzly bears; in other words, bears may preferentially seek out areas that are underperforming from a forest recovery perspective. Third, substantially more data were available for this study, which may better reveal selection patterns.

4.3. Satellite time series in RSF modeling

This study demonstrated the importance of spatially-explicit metrics of forest disturbance (by type) and recovery derived from satellite time series for modeling wildlife habitat selection in dynamic landscapes. While the base model of habitat selection performed well for not recently disturbed locations, it did poorly in disturbed areas ([Table 2](#)). Other studies have used stand age to represent disturbance, however age was often binned into coarse multi-year intervals and did not reflect variation in recovery within a given age-class (e.g., [Nielsen et al.](#),

[2004a](#); [Stewart et al., 2012](#); [Wielgus and Vernier, 2003](#)). Moreover, there can be a lag between disturbance and stand establishment ([Bradford et al., 2008](#)), and remote sensing technology is ideally suited to capture and quantify the change of forest conditions through time. By using a gap-free satellite annual time series we were able to reconstruct forest disturbance histories and create continuous variables associated with vegetation recovery that appear to reflect meaningful changes between seral stages during forest regeneration. For example, in harvested locations, probability of use tended to be lowest when spectral recovery was greater than 80%, with little change after that ([Fig. 5](#)). This value corresponds with findings by [White et al. \(2018\)](#) that spectral recovery values of 80% were highly correlated with airborne laser scanning metrics of canopy cover and tree height in boreal forests in southern Finland that were indicative of a return to forested conditions after harvesting. More work is needed to understand how spectral recovery relates to forest regeneration in naturally disturbed areas, especially following non-stand replacing disturbances, which likely represent a range of different causes and successional outcomes.

We also found strong non-linear interactions between satellite-derived indices representing vegetation structure (NBR) and greenness (GRN), demonstrating the importance of multiple spectral indices for modeling and mapping habitat selection. Some studies have concluded that remotely sensed vegetation indices do not correspond with grizzly bear habitat selection ([Stewart et al., 2012](#)) and are not correlated with the abundance of grizzly bears or their food resources ([Nielsen et al., 2016](#)). However, these aforementioned studies used a single index representing either greenness (GRN) or productivity (e.g., NDVI –

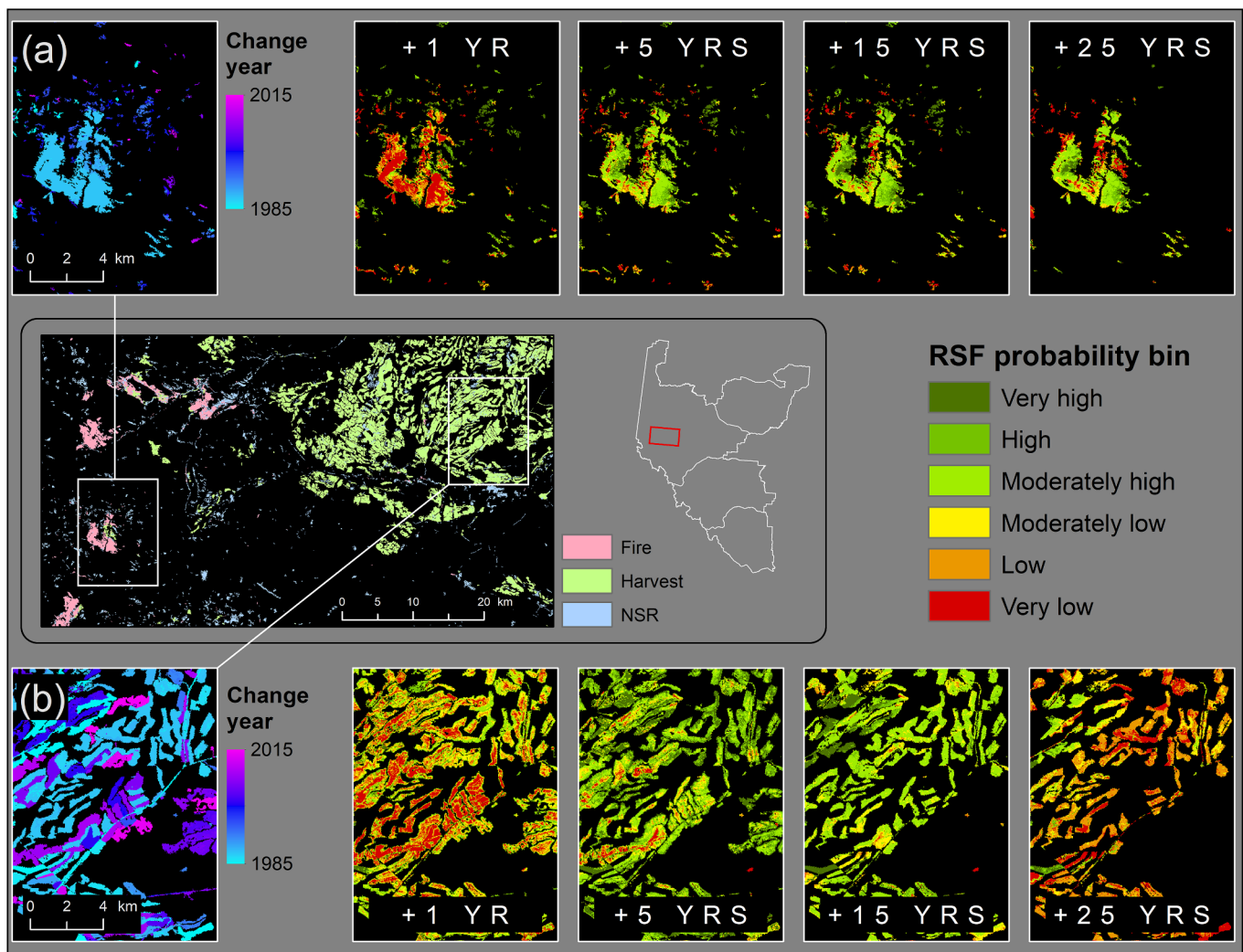


Fig. 7. Examples of change in probability of selection during Hyperphagia following disturbances. The center map is an inset within the Grande Cache BMA showing detected disturbances and their types (NSR = non-stand replacing) between 1985 and 2015. The top row (a) highlights an area of change following fire and bottom row (b) highlights change following forest harvesting. The far left panel of each row shows the change year in which disturbances were detected. The next four panels to the right show the binned predicted resource selection function (RFSF) probability at 1, 5, 15 and 25 years after disturbance. Note that detected disturbances that do not achieve a given years after disturbance by 2015 are not shown in that respective panel (e.g., a disturbance detected in 2009 could only be mapped for up to 6 years after disturbance, and thus is not shown in the +15 or +25 panels).

normalized difference vegetation index), neither of which are well correlated with forest structure variables.

We highlight the importance of including variables related to vegetation structure, such as NBR. In our large study, when NBR was high (i.e., greater than about 0.7), probability of use was low regardless of GRN. However, at intermediate values of NBR (0.3–0.6), grizzly bears were more likely to select for locations with higher GRN. NBR may be a particularly important indicator of berry producing shrubs, while GRN is likely more strongly related to herbaceous vegetation (i.e., forbs and grasses). During Mesophagia, when forbs and grasses are key food sources, probability of use was strongly related to GRN across all values of NBR. By contrast, during Hyperphagia, when berries are principle food source, probability of use was low at higher values of NBR irrespective of GRN values (Fig. 4a). We recommend further research on the use of both indices together to refine grizzly bear food models and in habitat selection modelling for other species.

4.4. Implications for forest management

The rapid decline in the probability of habitat use in previously harvested areas after about 15–20 years is most likely related to canopy

closure of managed (e.g., planted) coniferous trees and a transition away from early seral vegetation with abundant bear foods. Mature conifer-dominated stands have been shown to be unattractive to grizzly bears, despite potential benefits such as thermal cover (Pigeon et al., 2016), and field studies have shown that the presence of many vegetative bear foods, most notably blueberry (*Vaccinium* spp.), tended to be lower in older cutblocks (greater than 20–30 years) and negatively associated with canopy cover and distance to forest edge (Larsen et al., 2019; Nielsen et al., 2004b).

In our study area, canopy closure appears to be occurring more quickly after harvest compared to fires, a trend that has also been found in studies looking at the entirety of Canada's forest ecosystems (Hermosilla et al., 2018; White et al., 2017). Harvesting occurs only on treed sites and often in the most productive areas, and indeed we found slightly higher and less variable pre-NBR values in harvested compared to fire-disturbed locations. This likely contributes to the more rapid recovery relative to areas impacted by wildfire (Madoui et al., 2015). Moreover, successful forest regeneration after harvest is mandated by law on public forest land in Canada (Natural Resources Canada, 2018), and there has been a tendency toward forest management practices that encourage rapid regrowth of even-aged conifers, driven by both

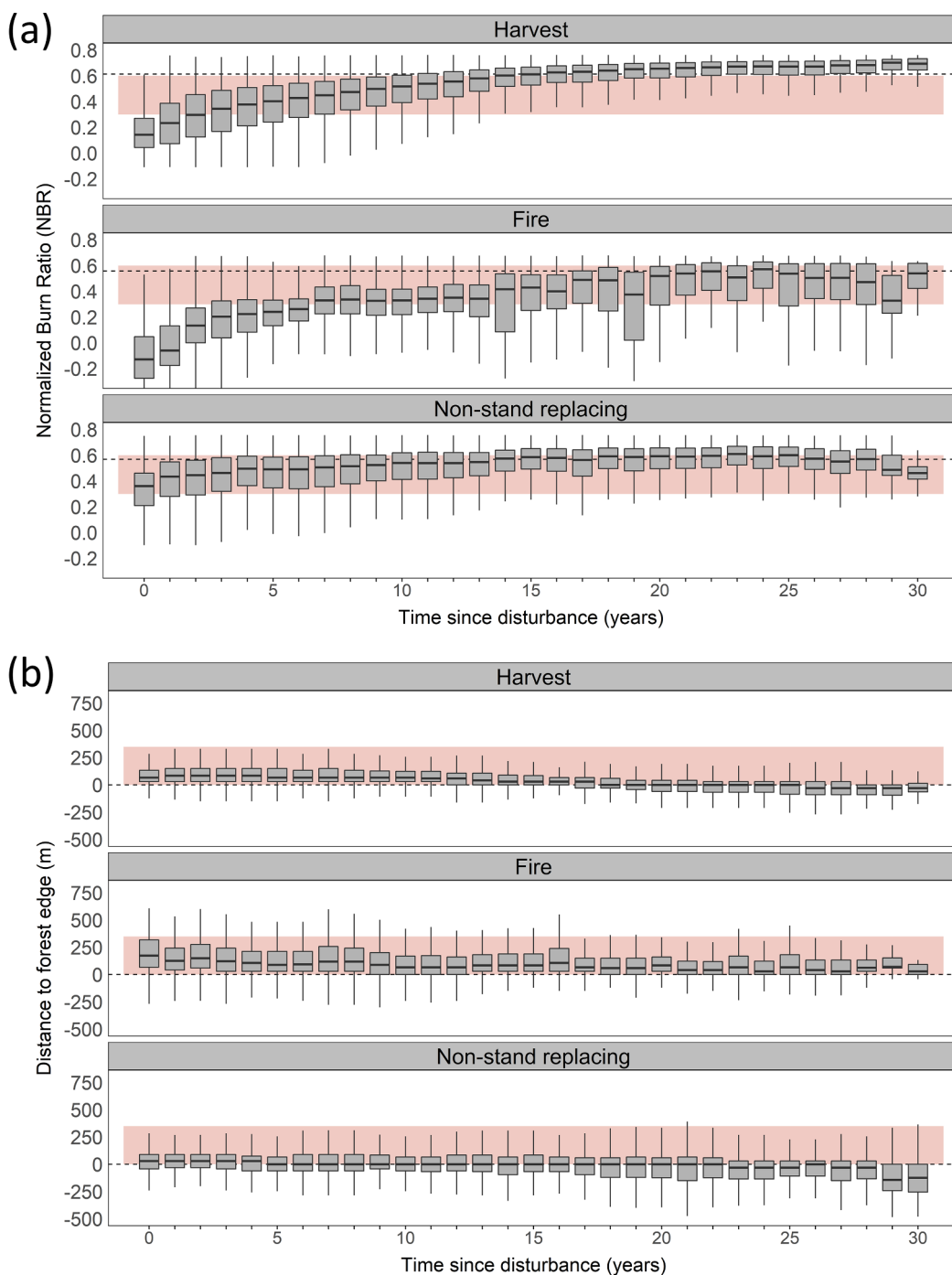


Fig. 8. Change in NBR and distance to forest edge following disturbance across available locations. Horizontal dotted lines for (a) indicate the average pre-disturbance Normalized Burn Ratio (NBR) value and for (b) indicate the forest edge (0 m distance). Negative values of distance to forest edge indicate locations inside the forest and positive values outside. Ranges in red correspond to the range of each variable for which resource selection function (RSF) models predicted high probability of use by grizzly bears (also see Fig. 4). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

government policies, as well as ecological and economic incentives (Drever et al., 2006; Lieffers et al., 2008). In Alberta, legislation requires that harvested areas return to 80% of pre-harvest stocking density within eight years, and require planting within two years if natural regeneration is not expected to achieve this (Alberta Agriculture and Forestry, 2018). As a result, over the last 25 years, about 80% of harvested areas in Alberta were planted or seeded, mostly with conifers (Canadian Council of Forest Ministers, 2018). Additionally, 12% of harvested areas were mechanically disturbed (e.g., scarified), and since 1999 when herbicide use became more common, an average of 41% of harvested areas were sprayed with herbicides to reduce competition from non-harvested species (Canadian Council of Forest Ministers, 2018).

These types of practices could be leading to a short time period (< 20 years) of increased habitat quality, followed by a relatively low

quality habitat state. Furthermore, the increase in habitat quality may be higher during Mesophagia than for Hypophagia or Hyperphagia. When natural disturbances were abundant, the likelihood of selecting harvested forests was higher during Mesophagia than during Hypophagia or Hyperphagia (Fig. 2). One possible explanation for this difference is that harvesting activities and post-harvest management are fostering important Mesophagia food sources and reducing the supply of foods important during Hypophagia and Hyperphagia. In Alberta, occurrence of roots, berries and ungulates – all of which are primarily consumed during Hypophagia and Hyperphagia – are negatively associated with mechanical soil disturbance and high canopy closure (Haeussler et al., 1999; Moola and Mallik, 1998; Nielsen et al., 2004b). By contrast, it has been shown that some herbaceous and graminoid foods often consumed during Mesophagia are positively associated with

soil disturbance (Haeussler et al., 1999; Nielsen et al., 2004b; Zager et al., 1983) and high canopy cover (Nielsen et al., 2004b). Other strategies to promote timber growth such as herbicide application may further promote the growth of grasses and herbicide resistant forbs such as cow parsnip (*Heracleum lanatum*) (Page et al., 2006; Sheppard, 1991), whereas berry-producing shrubs (e.g., *Vaccinium* spp.) are adversely affected by herbicides (Bovey, 1977; Moola and Mallik, 1998).

There has been a rise in natural disturbance-based forestry in North America to mimic disturbance patterns produced by wildfires to conserve biodiversity and wildlife habitat (Bose et al., 2014). However, such management has focused largely on spatial harvest patterns, partial cutting, and structure retention (Bose et al., 2014; Gustafsson et al., 2012), while post-harvest silviculture practices, particularly the timing and density of planting and release management strategies (e.g., herbicide application), has been given relatively less attention. Data were not available for this study to directly compare silvicultural management practices to grizzly bear food abundance and habitat selection. Such a comparison is needed to determine the effects of post-harvest vegetation management on grizzly bear habitat quality and foods, and provide more detailed management recommendations for forest harvesting and post-harvest forest recovery.

Additionally, the cumulative effects of fire suppression and rapid post-harvest forest regeneration on regional grizzly bear habitat quality and population health remain unknown. Scenario modeling using results from this study and others would help to understand the trade-offs between competing interests and objectives. For example, prescribed burning and reduced fire suppression in areas where communities and infrastructure are not at risk could increase grizzly bear foraging opportunities. Focusing these activities around cutblocks could have the added benefit of drawing grizzly bears away from forestry roads and decreasing the likelihood of negative bear-human interactions. It is also possible that fires in productive commercial forests may yield greater food resources for grizzly bears compared to the more variable and high-elevation areas where fires are typically allowed to burn without suppression (i.e., protected parks). Avoiding salvage logging and subsequent replanting after low-intensity fires and non-stand replacing disturbances may prolong attractive grizzly bear habitat. Reducing or delaying regeneration efforts after harvest in strategic areas where fires are deemed unacceptable may also be beneficial, though trade-offs are likely to exist between other ecological and economic objectives, and these would need to be taken into consideration. Expanded research on the relationship between grizzly bear foods, body condition and post-harvest management is advisable, especially for understudied practices which include the timing and density of restocking, and the use of release strategies such as herbicide application.

Acknowledgements

This research was supported by the Grizzly-PAW project (NSERC File: CRDPJ 486175 – 15, Grantee: N.C. Coops, FRM, UBC), in collaboration with fRI Research and FRIAA, Alberta Newsprint Company, Canfor, Cenovus, Repsol, Seven Generations Energy, Shell Canada, TransCanada Pipelines, Teck Resources, West Fraser, Westmoreland Coal, and Weyerhaeuser. More information can be found at <http://paw.forestry.ubc.ca/>.

References

- Alberta Agriculture and Forestry, 2018. Reforestation Standard of Alberta. Edmonton, Alberta.
- Andison, D.W., 1998. Temporal patterns of age-class distributions on foothills landscapes in Alberta. *Ecography (Cop.)* 21, 543–550. <https://doi.org/10.1111/j.1600-0587.1998.tb00446.x>.
- Avgar, T., Lele, S.R., Keim, J.L., Boyce, M.S., 2017. Relative selection strength: quantifying effect size in habitat- and step-selection inference. *Ecol. Evol.* 7, 5322–5330. <https://doi.org/10.1002/ece3.3122>.
- Bartels, S.F., Chen, H.Y.H., Wulder, M.A., White, J.C., 2016. Trends in post-disturbance recovery rates of Canada's forests following wildfire and harvest. *For. Ecol. Manage.* 361, 194–207. <https://doi.org/10.1016/j.foreco.2015.11.015>.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 51. <https://doi.org/10.18637/jss.v067.i01>.
- Berland, A., Nelson, T., Stenhouse, G., Graham, K., Cranston, J., 2008. The impact of landscape disturbance on grizzly bear habitat use in the Foothills Model Forest, Alberta, Canada. *For. Ecol. Manage.* 256, 1875–1883. <https://doi.org/10.1016/j.foreco.2008.07.019>.
- Bose, A.K., Harvey, B.D., Brais, S., Beaudet, M., Leduc, A., 2014. Constraints to partial cutting in the boreal forest of Canada in the context of natural disturbance-based management: a review. *Forestry* 87, 11–28. <https://doi.org/10.1093/forestry/cpt047>.
- Boulanger, J., Cattet, M., Nielsen, S.E., Stenhouse, G., Cranston, J., 2013. Use of multi-state models to explore relationships between changes in body condition, habitat and survival of grizzly bears *Ursus arctos horribilis*. *Wildlife Biol.* 19, 274–288. <https://doi.org/10.2981/12-088>.
- Boulanger, J., Stenhouse, G.B., Margalida, A., 2014. The impact of roads on the demography of grizzly bears in Alberta. *PLoS One* 9, 1–22. <https://doi.org/10.1371/journal.pone.0115535>.
- Bovey, R.W., 1977. Response of Selected Woody Plants in the United States to Herbicides. Washington, D.C.
- Boyce, M.S., Vernier, P.R., Nielsen, S.E., Schmiegelow, F.K.A., 2002. Evaluating resource selection functions. *Ecol. Modell.* 157, 281–300. [https://doi.org/10.1016/S0304-3800\(02\)00200-4](https://doi.org/10.1016/S0304-3800(02)00200-4).
- Bradford, J.B., Birdsey, R.A., Joyce, L.A., Ryan, M.G., 2008. Tree age, disturbance history, and carbon stocks and fluxes in subalpine Rocky Mountain forests. *Glob. Chang. Biol.* 14, 2882–2897. <https://doi.org/10.1111/j.1365-2486.2008.01686.x>.
- Cameron, A.C., Gelbach, J.B., Miller, D.L., 2011. Robust inference with multiway clustering. *J. Bus. Econ. Stat.* 29, 238–249. <https://doi.org/10.1198/jbes.2010.07136>.
- Canadian Council of Forest Ministers, 2018. National Forestry Database [WWW Document]. URL <http://www.nfdp.ccfm.org/> (accessed 11.20.18).
- Chavardès, R.D., Daniels, L.D., Gedalof, Z., Anderson, D.W., 2018. Human influences superseded climate to disrupt the 20th century fire regime in Jasper National Park, Canada. *Dendrochronologia* 48, 10–19. <https://doi.org/10.1016/j.dendro.2018.01.002>.
- Clark, D.A., Slocombe, D.S., 2011. Grizzly Bear conservation in the Foothills Model Forest: appraisal of a collaborative ecosystem management effort. *Policy Sci.* 44, 1–11. <https://doi.org/10.1007/s11077-010-9118-y>.
- Cohen, W.B., Spies, T.A., 1992. Estimating structural attributes of Douglas-Fir/Western Hemlock forest stands from Landsat and SPOT imagery. *Remote Sens. Environ.* 41, 1–17. <https://doi.org/10.1007/BF00721230>.
- Courtois, R., Dussault, C., Potvin, F., Daigle, G., 2002. Habitat selection by mosse (Alces alces) in clear-cut landscapes. *Alces* 38, 177–192.
- Crist, E.P., Ciccone, R.C., 1984. A physically-based transformation of Thematic Mapper data - the TM tasselled cap. *IEEE Trans. Geosci. Remote Sens.* GE-22, 256–263.
- Cristescu, B., Stenhouse, G.B., Boyce, M.S., 2014. Grizzly bear ungulate consumption and the relevance of prey size to caching and meat sharing. *Anim. Behav.* 92, 133–142. <https://doi.org/10.1016/j.anbehav.2014.03.020>.
- Drever, C.R., Peterson, G., Messier, C., Bergeron, Y., Flannigan, M., 2006. Can forest management based on natural disturbances maintain ecological resilience? *Can. J. For. Res.* 36, 2285–2299. <https://doi.org/10.1139/x06-132>.
- ESRI, 2017. ArcGIS Desktop: Release 10.5.
- Festa-Bianchet, M., 2010. Status of the Grizzly Bear (*Ursus arctos*) in Alberta: Update 2010, Wildlife Status Report No.37 (Update 2010). Edmonton, AB.
- Fieberg, J., 2007. Kernel density estimators of home range: Smoothing and the autocorrelation red herring. *Ecology* 88, 1059–1066. <https://doi.org/10.1890/06-0930>.
- Frolking, S., Palace, M.W., Clark, D.B., Chambers, J.Q., Shugart, H.H., Hurr, G.C., 2009. Forest disturbance and recovery: a general review in the context of spaceborne remote sensing of impacts on aboveground biomass and canopy structure. *J. Geophys. Res. Biogeosci.* 114. <https://doi.org/10.1029/2008JG000911>.
- Griffiths, P., Kuemmerle, T., Baumann, M., Radeloff, V.C., Abrudan, I.V., Lieskovsky, J., Munteanu, C., Ostapowicz, K., Hostert, P., 2014. Forest disturbances, forest recovery, and changes in forest types across the carpathian ecoregion from 1985 to 2010 based on landsat image composites. *Remote Sens. Environ.* 151, 72–88. <https://doi.org/10.1016/j.rse.2013.04.022>.
- Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J., Lindenmayer, D.B., Löhmus, A., Pastur, G.M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, W.J.A., Wayne, A., Franklin, J.F., 2012. Retention forestry to maintain multifunctional forests: a world perspective. *Bioscience* 62, 633–645. <https://doi.org/10.1525/bio.2012.62.7.6>.
- Haeussler, S., Bedford, L., Boateng, J.O., MacKinnon, A., 1999. Plant community responses to mechanical site preparation in northern interior British Columbia. *Can. J. For. Res.* 29, 1084–1100. <https://doi.org/10.1139/cjfr-29-7-1084>.
- Hermosilla, T., Wulder, M.A., White, J.C., Coops, N.C., Hobart, G.W., 2018. Disturbance-Informed Annual Land Cover Classification Maps of Canada's Forested Ecosystems for a 29-Year Landsat Time Series. *Can. J. Remote Sens.* 44, 67–87. <https://doi.org/10.1080/07038992.2018.1437719>.
- Hermosilla, T., Wulder, M.A., White, J.C., Coops, N.C., Hobart, G.W., 2015a. An integrated Landsat time series protocol for change detection and generation of annual gap-free surface reflectance composites. *Remote Sens. Environ.* 158, 220–234. <https://doi.org/10.1016/j.rse.2014.11.005>.
- Hermosilla, T., Wulder, M.A., White, J.C., Coops, N.C., Hobart, G.W., 2015b. Regional detection, characterization, and attribution of annual forest change from 1984 to 2012 using Landsat-derived time-series metrics. *Remote Sens. Environ.* 170, 121–132. <https://doi.org/10.1016/j.rse.2015.09.004>.
- Hermosilla, T., Wulder, M.A., White, J.C., Coops, N.C., Hobart, G.W., Campbell, L.B., 2016. Mass data processing of time series Landsat imagery: pixels to data products for

- forest monitoring. *Int. J. Digit. Earth* 9, 1035–1054. <https://doi.org/10.1080/17538947.2016.1187673>.
- Ironside, K.E., Mattson, D.J., Arundel, T.R., Hansen, J.R., 2017. Is GPS telemetry location error screening beneficial? *Wildlife Biol.* 17. <https://doi.org/10.2981/wlb.00229>.
- Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61, 65–71. <https://doi.org/10.2307/1937156>.
- Key, C.H., Benson, N.C., 2006. *Landscape Assessment: Sampling and Analysis Methods*. USDA Forest Service General Technical Report RMRS-GTR-164-CD. <https://doi.org/10.1002/app.1994.070541203>.
- Koper, N., Manseau, M., 2012. A guide to developing resource selection functions from telemetry data using generalized estimating equations and generalized linear mixed models. *Rangifer* 32, 195. <https://doi.org/10.7557/2.32.2.2269>.
- Lamb, C.T., Mowat, G., Reid, A., Smit, L., Proctor, M., McLellan, B.N., Nielsen, S.E., Boutin, S., 2018. Effects of habitat quality and access management on the density of a recovering grizzly bear population. *J. Appl. Ecol.* 1–12. <https://doi.org/10.1111/1365-2664.13056>.
- Larsen, T.A., Nielsen, S.E., Cranston, J., Stenhouse, G.B., 2019. Do remnant retention patches and forest edges increase grizzly bear food supply? *For. Ecol. Manage.* 433, 741–761. <https://doi.org/10.1016/j.foreco.2018.11.031>.
- Lieffers, V.J., Armstrong, G.W., Stadt, K.J., Marenholtz, E.H., 2008. Forest regeneration standards: are they limiting management options for Alberta's boreal mixedwoods? *For. Chron.* 84, 76–82. <https://doi.org/10.5558/tfc84076-1>.
- Liu, Q., Liu, G., Huang, C., Xie, C., Chu, L., Shi, L., 2016. Comparison of tasseled cap components of images from Landsat 5 Thematic Mapper and Landsat 7 Enhanced Thematic Mapper Plus. *J. Spat. Sci.* 61, 351–365. <https://doi.org/10.1080/14498596.2015.1124810>.
- Madoui, A., Gauthier, S., Leduc, A., Bergeron, Y., Valeria, O., 2015. Monitoring forest recovery following wildfire and harvest in boreal forests using satellite imagery. *Forests* 6, 4105–4134. <https://doi.org/10.3390/f6114105>.
- Mattson, D.J., Merrill, T., 2002. Extirpations of grizzly bears in the contiguous United States, 1850–2000. *Conserv. Biol.* 16, 1123–1136. <https://doi.org/10.1046/j.1523-1739.2002.00414.x>.
- McLellan, B.N., Hovey, F.W., 2001. Habitats selected by grizzly bears in a multiple use landscape. *J. Wildl. Manage.* 65, 92–99.
- McLellan, B.N., Hovey, F.W., Mace, R.D., Woods, J.G., Carney, D.W., Gibeau, M.L., Wakkinen, W.L., Kasworm, W.F., 1999. Rates and causes of grizzly bear mortality in the interior mountains of British Columbia, Alberta, Montana, Washington, and Idaho. *J. Wildl. Manage.* 63, 911. <https://doi.org/10.2307/3802805>.
- Milner, J.M., van Beest, F.M., Storaas, T., 2013. Boom and bust of a moose population: a call for integrated forest management. *Eur. J. For. Res.* 132, 959–967. <https://doi.org/10.1007/s10342-013-0727-9>.
- Moola, F.M., Mallik, A.U., 1998. Morphological plasticity and regeneration strategies of velvet leaf blueberry (*Vaccinium myrtilloides* Michx.) following canopy disturbance in boreal mixedwood forests. *For. Ecol. Manage.* 111, 35–50. [https://doi.org/10.1016/S0378-1127\(98\)00306-5](https://doi.org/10.1016/S0378-1127(98)00306-5).
- Mowat, G., Heard, D.C., Seip, D.R., Poole, K.G., Stenhouse, G., Stenhouse, K.G., Paetkau, D.W., 2005. Grizzly *Ursus arctos* and black bear *U. americanus* densities in the interior mountains of North America. *Wildlife Biol.* 11, 31–48. [https://doi.org/10.2981/0909-6396\(2005\)11\[31:GUAABB\]2.0.CO;2](https://doi.org/10.2981/0909-6396(2005)11[31:GUAABB]2.0.CO;2).
- Munro, R.H.M., Nielsen, S.E., Price, M.H., Stenhouse, G.B., Boyce, M.S., 2006. Seasonal and diel patterns of grizzly bear diet and activity in West-Central Alberta. *J. Mammal.* 87, 1112–1121. <https://doi.org/10.1644/05-MAMM-A-410R3.1>.
- Natural Regions Committee, 2006. *Natural Regions and Subregions of Alberta*. Pub. No. T/852. doi:Pub. No. T/852.
- Natural Resources Canada, 2018. *The State of Canada's Forests: Annual Report 2018*.
- Nielsen, S.E., Boyce, M.S., Stenhouse, G.B., 2004a. Grizzly bears and forestry: I. Selection of clearcuts by grizzly bears in west-central Alberta, Canada. *For. Ecol. Manage.* 199, 51–65. <https://doi.org/10.1016/j.foreco.2004.04.014>.
- Nielsen, S.E., Cattet, M.R.L., Boulanger, J., Cranston, J., Mcdermid, G.J., Shafer, A.B.A., 2013. Environmental, biological and anthropogenic effects on grizzly bear body size: temporal and spatial considerations. *BMC Ecol.* 13, 12. <https://doi.org/10.1186/1472-6785-13-31>.
- Nielsen, S.E., Cranston, J., Stenhouse, G.B., 2009. Identification of priority areas for grizzly bear conservation and recovery in Alberta, Canada. *J. Conserv. Plan.* 5, 38–60.
- Nielsen, S.E., Larsen, T.A., Stenhouse, G.B., Coogan, S.C.P., 2016. Complementary food resources of carnivory and frugivory affect local abundance of an omnivorous carnivore. *Oikos* 1–12. <https://doi.org/10.1111/oik.03144>.
- Nielsen, S.E., McDermid, G., Stenhouse, G.B., Boyce, M.S., 2010. Dynamic wildlife habitat models: seasonal foods and mortality risk predict occupancy-abundance and habitat selection in grizzly bears. *Biol. Conserv.* 143, 1623–1634. <https://doi.org/10.1016/j.biocon.2010.04.007>.
- Nielsen, S.E., Munro, R.H.M., Bainbridge, E.L., Stenhouse, G.B., Boyce, M.S., 2004b. Grizzly bears and forestry: II. Distribution of grizzly bear foods in clearcuts of west-central Alberta, Canada. *For. Ecol. Manage.* 199, 67–82. <https://doi.org/10.1016/j.foreco.2004.04.015>.
- Page, N.A., Wall, R.E., Darbyshire, S.J., Mulligan, G.a., 2006. The Biology of invasive alien plants in Canada. *Heracleum mantegazzianum* Sommier & Levier. *Can. J. Plant Sci.* 86, 569–589. <https://doi.org/10.4141/P05-158>.
- Pascual, C., García-Abriol, A., Cohen, W.B., Martín-Fernández, S., 2010. Relationship between LiDAR-derived forest canopy height and Landsat images. *Int. J. Remote Sens.* 31, 1261–1280. <https://doi.org/10.1080/01431160903380656>.
- Peng, C., Ma, Z., Lei, X., Zhu, Q., Chen, H., Wang, W., Liu, S., Li, W., Fang, X., Zhou, X., 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nat. Clim. Chang.* 1, 467–471. <https://doi.org/10.1038/nclimate1293>.
- Pickell, P.D., Anderson, D.W., Coops, N.C., Gergel, S.E., Marshall, P.L., 2015. The spatial patterns of anthropogenic disturbance in the western Canadian boreal forest following oil and gas development. *Can. J. For. Res.* 45, 732–743.
- Pickell, P.D., Hermosilla, T., Frazier, R.J., Coops, N.C., Wulder, M.A., 2016. Forest recovery trends derived from Landsat time series for North American boreal forests. *Int. J. Remote Sens.* 37, 138–149. <https://doi.org/10.1080/2150704X.2015.1126375>.
- Pigeon, K.E., Cardinal, E., Stenhouse, G.B., Côté, S.D., 2016. Staying cool in a changing landscape: the influence of maximum daily ambient temperature on grizzly bear habitat selection. *Oecologia* 181, 1101–1116. <https://doi.org/10.1007/s00442-016-3630-5>.
- Potvin, F., Breton, L., Courtois, R., 2005. Response of beaver, moose, and snowshoe hare to clear-cutting in a Quebec boreal forest: a reassessment 10 years after cut. *Can. J. For. Res.* 35, 151–160. <https://doi.org/10.1139/x04-151>.
- R Core Team, 2016. *R: A Language and Environment for Statistical Computing*.
- Rhemtulla, J.M., 1999. *Eighty Years of Change: The Montane Vegetation of Jasper National Park*. University of Alberta.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and ecological effects of the world's largest carnivores. *Science* (80-) 343 (6167), 1241484. <http://www.sciencemag.org/cgi/doi/10.1126/science.1241484><https://doi.org/10.1126/science.1241484>.
- Roeber, C.L., Boyce, M.S., Stenhouse, G.B., 2008. Grizzly bears and forestry: I. road vegetation and placement as an attractant to grizzly bears. *For. Ecol. Manage.* 256, 1253–1261. <https://doi.org/10.1016/j.foreco.2008.06.040>.
- Safranyik, L., Carroll, A.L., Régnière, J., Langor, D.W., Riel, W.G., Shore, T.L., Peter, B., Cooke, B.J., Nealis, V.G., Taylor, S.W., 2010. Potential for range expansion of mountain pine beetle into the boreal forest of North America. *Can. Entomol.* 142, 415–442. <https://doi.org/10.4039/n08-CPA01>.
- Sheppard, A.W., 1991. *Heracleum Sphondylium* L. *J. Ecol.* 79, 235–258.
- Stelfox, J.G., Lynch, G.M., McGillis, J.R., 1976. Effects of clearcut logging on wild ungulates in the central Albertan foothills. *For. Chron.* 65–70. <https://doi.org/10.5558/tfc52065-2>.
- Stewart, B.P., Nelson, T.A., Laberee, K., Nielsen, S.E., Wulder, M.A., Stenhouse, G., 2013. Quantifying grizzly bear selection of natural and anthropogenic edges. *J. Wildl. Manage.* 77, 957–964. <https://doi.org/10.1002/jwmg.535>.
- Stewart, B.P., Nelson, T.A., Wulder, M.A., Nielsen, S.E., Stenhouse, G., 2012. Impact of disturbance characteristics and age on grizzly bear habitat selection. *Appl. Geogr.* 34, 614–625. <https://doi.org/10.1016/j.apgeog.2012.03.001>.
- Strong, W.L., Gates, C.C., 2006. Herbicide-induced changes to ungulate forage habitat in western Alberta, Canada. *For. Ecol. Manage.* 222, 469–475. <https://doi.org/10.1016/j.foreco.2005.10.036>.
- Thorpe, H.C., Daniels, L.D., 2012. Long-term trends in tree mortality rates in the Alberta foothills are driven by stand development. *Can. J. For. Res.* 42, 1687–1696. <https://doi.org/10.1139/x2012-104>.
- Tirmenstein, D., 1990. *Vaccinium myrtilloides* [WWW Document]. *Fire Eff. Inf. Syst.* [Online]. URL <https://www.fs.fed.us/database/feis/plants/shrub/vacmyrt/all.html> (accessed 10.9.18).
- Tomm, H.O., Beck Jr., J.A., Hundson, R.J., 1981. Response of wild ungulates to logging practices in Alberta. *Can. J. For. Res.* 11, 606–614. <https://doi.org/10.1139/x81-083>.
- White, J.C., Saarinen, N., Kankare, V., Wulder, M.A., Hermosilla, T., Coops, N.C., Pickell, P.D., Holopainen, M., Hyypää, J., Vastaranta, M., 2018. Confirmation of post-harvest spectral recovery from Landsat time series using measures of forest cover and height derived from airborne laser scanning data. *Remote Sens. Environ.* 216, 262–275. <https://doi.org/10.1016/j.rse.2018.07.004>.
- White, J.C., Wulder, M.A., Gómez, C., Stenhouse, G., 2011. A history of habitat dynamics: characterizing 35 years of stand replacing disturbance. *Can. J. Remote Sens.* 37, 234–251.
- White, J.C., Wulder, M.A., Hermosilla, T., Coops, N.C., Hobart, G.W., 2017. A nationwide annual characterization of 25 years of forest disturbance and recovery for Canada using Landsat time series. *Remote Sens. Environ.* 194, 303–321. <https://doi.org/10.1016/j.rse.2017.03.035>.
- Wielgus, R.B., Vernier, P.R., 2003. Grizzly bear selection of managed and unmanaged forests in the Selkirk Mountains. *Can. J. For. Res.* 33, 822–829. <https://doi.org/10.1139/x03-003>.
- Zager, P., Jonkel, C., Habeck, J., 1983. *Logging and wildfire influence on grizzly bear habitat in Northwest Montana*. In: *International Conference on Bear Research and Management*. Madison, Wisconsin, USA, pp. 124–132.
- Zedrosser, A., Steyaert, S.M.J.G., Gossow, H., Swenson, J.E., 2011. Brown bear conservation and the ghost of persecution past. *Biol. Conserv.* 144, 2163–2170. <https://doi.org/10.1016/j.biocon.2011.05.005>.