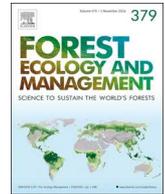




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## Do remnant retention patches and forest edges increase grizzly bear food supply?

Terrence A. Larsen<sup>a,\*</sup>, Scott E. Nielsen<sup>b</sup>, Jerome Cranston<sup>c</sup>, Gordon B. Stenhouse<sup>a</sup><sup>a</sup> 1176 Switzer Drive, Hinton, Alberta T7V 1V3, Canada<sup>b</sup> Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada<sup>c</sup> CW 405, Biological Sciences Building, University of Alberta, Edmonton, Alberta T6G 2E9, Canada

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## ABSTRACT

Grizzly bears should benefit from forest harvesting strategies that emulate patterns of natural disturbance, such as wildfire, presumably because of increased foraging opportunities associated with open and edge habitats. Several studies have linked early seral habitats associated with natural and anthropogenic disturbances to increased food supply for grizzly bear. However, few have quantitatively evaluated whether food supply is higher along forest edges, particularly edges created by different forest harvesting strategies such as structure retention. Here we tested whether grizzly bear food supply was: 1) more common/abundant along forest harvest (cutblock) edges; 2) similar between undisturbed forest matrix (uncut) undisturbed forest remnants (i.e., retention patches) that were situated within forest harvests; and 3) similar in terms of responses relative to retention and forest harvest edges. To address these questions, we measured the distribution and abundance of plant-based food resources used by grizzly bears along edge distance gradients associated with three forest treatments (cutblock, uncut forest, and retention patch) in Alberta, Canada. We then used information theory to compare models and evaluate support for factors. We found that blueberry (*Vaccinium membranaceum*, *V. myrtilloides*, and *V. vitis-idaea*) shrubs, which are known to be sensitive to mechanical damage and soil disturbance from harvest and post-harvest site preparation, were more common/abundant near young ( $\leq 20$  years) forest edges. Conversely, raspberry (*Rubus idaeus*) shrubs, horsetail (*Equisetum arvense*), and cow parsnip (*Heracleum lanatum*), which are known to be positively associated with soil disturbance, were generally more common/abundant away from forest edges. Blueberry, fruit production was highest at forest harvest edges and lowest in older cutblocks, as well as retention patches, which we showed contained fewer lodgepole pine (*Pinus contorta*) trees and more deciduous species. These results support the contention that understory disturbance, environmental conditions (e.g. light availability), and forest tree species composition could explain our research findings. As part of stand-level prescriptions, we recommend that forest managers consider maintaining uncut forest adjacent to cutblocks for up to 20 years post-harvest, and create more and smaller retention patches to increase the amount of forest edge. We also recommend that criteria be developed for selecting the spatial location of forest edges and retention patches such that blueberry shrubs are common/abundant in the undisturbed forest. This research demonstrated that forest harvesting strategies can increase food supply for grizzly bears and thus support recovery efforts of this provincially threatened species.

## 1. Introduction

Natural disturbance-based forestry has become a more common management practice in temperate and boreal forest regions of North America (e.g. Bergeron and Harvey, 1997; Bergeron et al., 1999; Lieffers et al., 1996; Work et al., 2003). In particular, the implementation of forest harvesting strategies that mimic the natural

variability of wildfire are now commonly used to promote ecologically sustainable forest management and to help conserve forest biodiversity (see reviews Bose et al., 2014; Burton et al., 2006; Kuuluvainen and Grenfell, 2012; Long, 2009; Patry et al., 2013; Work et al., 2003). Conceptually, this approach assumes that organisms, which have adapted to natural disturbance regimes, would be better able to persist in landscapes if forest harvesting strategies resembled natural

\* Corresponding author.

E-mail addresses: [tlarsen@friresearch.ca](mailto:tlarsen@friresearch.ca) (T.A. Larsen), [scott@ualberta.ca](mailto:scott@ualberta.ca) (S.E. Nielsen), [cranston@ualberta.ca](mailto:cranston@ualberta.ca) (J. Cranston), [gstenhouse@friresearch.ca](mailto:gstenhouse@friresearch.ca) (G.B. Stenhouse).

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disturbance events (Hunter, 1993).

Structure retention, the process of leaving residual materials such as dead or decaying wood, shrubs, or trees following timber harvest, has been widely adopted by forest managers in Canada and the United States as an alternative to clearcutting (Gustafsson et al., 2012; Work et al., 2003). In practice, structure retention aims to emulate the pattern of wildfire skips where heterogeneous patterns of unburned forest remnants are left behind. These biological and physical legacies of pre-harvest forest conditions retained within harvest blocks are thought to maintain structural complexity, species diversity and composition, and processes and function of forest ecosystems (Lindenmayer et al., 2012). The ecological benefits of retention patches have been investigated and confirmed for a variety of taxa – notably small mammals (Sullivan and Sullivan, 2001; Sullivan et al., 2008), birds (Harrison et al., 2005; Lance and Phinney, 2001; Stuart-Smith et al., 2006), insects (Jacobs et al., 2007; Work et al., 2010), and plants (Caners et al., 2010; Craig and Macdonald, 2009; MacDonald and Fenniak, 2007) – how this practice affects populations of large mammals, and in particular carnivores, remains largely unknown.

Grizzly bears (*Ursus arctos*) are a species likely to benefit from forest harvesting activities that resemble wildfire because of increased foraging opportunities associated with early seral and edge habitat (Hamer and Herrero, 1987a; Mattson, 1997; Mattson et al., 2002; Nielsen et al., 2004c). This is particularly true in forested environments where fire suppression over the past century has led to widespread late seral stands and reduced food supply for bears (Nielsen et al., 2004c; Zager et al., 1983). Grizzly bears are omnivorous and therefore capable of consuming a wide variety of food resource types including roots, tubers, herbs, fruits, insects, ungulates, small mammals, and even fishes; however, plant-based foods tend to be a major dietary component of interior bear populations (McLellan and Hovey, 1995; Mowat and Heard, 2006; Munro et al., 2006). However, less food available to grizzly bears at local and regional levels may negatively influence female body condition and consequently reproductive success and therefore lower ecosystem productivity and bear population size (Ferguson and McLoughlin, 2000; Hertel et al., 2017; López-Alfaro et al., 2015; Mowat et al., 2013; Zedrosser et al., 2006).

In Alberta, Canada, where natural forest openings are lacking, grizzly bears tend to be attracted to forest harvests and forest harvest edges (Nielsen et al., 2004a; Stewart et al., 2013a). Because of these relationships, forest harvesting is likely to improve habitat quality into the future due to an increase in early seral forest and forest edge (Nielsen et al. 2008). This is supported by previous research that has shown increased food supply in forest harvests, and that grizzly bears were more likely to see gains in body condition that utilised regenerating forests (Boulanger et al., 2013). Grizzly bears may further benefit from forest edges presumably due to increased food supply that is in close proximity to cover for resting or meeting thermal requirements (Cristescu et al., 2013; Munro et al., 2006; Pigeon et al., 2016). However, this hypothesis has yet to be tested with empirical data. Recently, Nielsen et al. (2017) showed that local grizzly bear abundance estimated using DNA-based methods was positively correlated with complementary resources; buffaloberry (*Shepherdia canadensis*) fruit as a key source of carbohydrate fruit and ungulate matter as a key source of protein and lipid. As such, forest management planning now considers measures of food supply (habitat), and its effects on survival, assuming a positive relationship between food resources and local population abundance (Nielsen et al., 2017, 2010). Understanding if food supply is increased along forest edges and within retention patches would inform the design of silvicultural treatments as a means to ensure long term habitat supply and recovery of a provincially threatened species.

The primary purpose of this research was to test whether grizzly bear food supply was higher along forest edges created by forest harvesting in west-central, Alberta, Canada. To achieve this, we collected distribution and abundance data on select forb and shrub species

known to be seasonally important foods utilised by grizzly bears in the region (Munro et al., 2006). More specifically, we collected bear food data at specific distances from the edges or boundaries between three forest treatment types (forest harvest [cutblock], undisturbed forest matrix [uncut forest], and remnant undisturbed forest matrix situated within a cutblock [retention patch]). If grizzly bear food supply was higher near forest edges, we predicted a negative relationship between edge distance and the occurrence/abundance of bear foods. Second to this, we tested whether food supply would be similar between uncut forests and retention patches, and whether edge distance responses would be similar between cutblock-retention and cutblock-uncut forest edge types. In this case, if food supply and edge distance responses were not different, we predicted no difference in bear food distribution/abundance and similar responses to edge distance. In answering these questions, we identify how forest harvesting strategies can be used to manage grizzly bear food supply and thus inform policy and management on forest edges and the use of retention patches in natural disturbance-based forestry.

## 2. Materials and methods

### 2.1. Study area

The study area encompasses part of the southern portion of Weyerhaeuser Forest Management Agreement (FMA) area in west-central Alberta, Canada (Fig. 1). Terrain, vegetation, and climate of the area were characteristic of the Subalpine (lower zone) and Upper Foothills Natural Subregions (Downing and Pettapiece, 2006). The higher elevation Subalpine has more rugged terrain transitioning at lower elevations to more rolling terrain of the Upper Foothills Region (Downing and Pettapiece, 2006). Forests are dominated by fire origin lodgepole pine (*Pinus contorta*) and black spruce (*Picea mariana*) that often co-occur. Stands of white spruce (*Picea glauca*) and deciduous species (*Populus tremuloides*, *P. balsamifera*) are less common than pine and tend to be found at lower elevations with white spruce predominantly found along riparian areas and deciduous and mixed stands often restricted to southern and western aspects. Mean annual temperature and precipitation ranges from  $-0.1^{\circ}\text{C}$  and 755.5 mm in the Subalpine to  $1.3^{\circ}\text{C}$  and 632.4 mm in the Upper Foothills regions.

### 2.2. Retention patch mapping and edge delineation

We used spatial data layers (e.g. Alberta Vegetation Inventory) provide by Weyerhaeuser to identify forested stands (polygons) that have been harvested (cut) or remained unharvested (uncut [fire origin]; > 43 years) (Nesby, 1997). To identify in-block retention of trees, we used three data sources based on visual examinations of high resolution orthophotos (i.e. SPOT and Landsat). This included: A) digitized dispersed (single) trees ( $\geq 15\text{ m}$  in height and  $< 0.5\text{ ha}$ ) or groups (patches) of trees ( $\geq 0.5\text{ ha}$ ) where the purpose was to map and quantify retention; B) digitized cutblocks where the purpose was to delineate harvested area boundaries including patches of retention; and C) a Light Detection and Ranging (Lidar) technique that we developed as part of this study.

To map retention using airborne Lidar data, we considered cutblocks harvested after 1990 because retention was difficult to differentiate from post-harvest regeneration in older cutblocks. We then used the following steps to delineate retention patches: 1) eliminated the inner 20 m boundary (edge) of each cutblock; 2) converted the remaining cutblock area to a raster (4 m pixel) and clipped a Lidar canopy height model (full feature surface subtracted from bare earth surface); 3) converted pixels of vegetation height ( $\geq 10\text{ m}$  represents uncut forest) to point features; and 4) buffered (6 m) features to approximate tree crowns and merged those with overlapping tree crowns to define retention patches. Before merging patches from the three data sets, we buffered (3 m) the point features (single trees) from A) to approximate

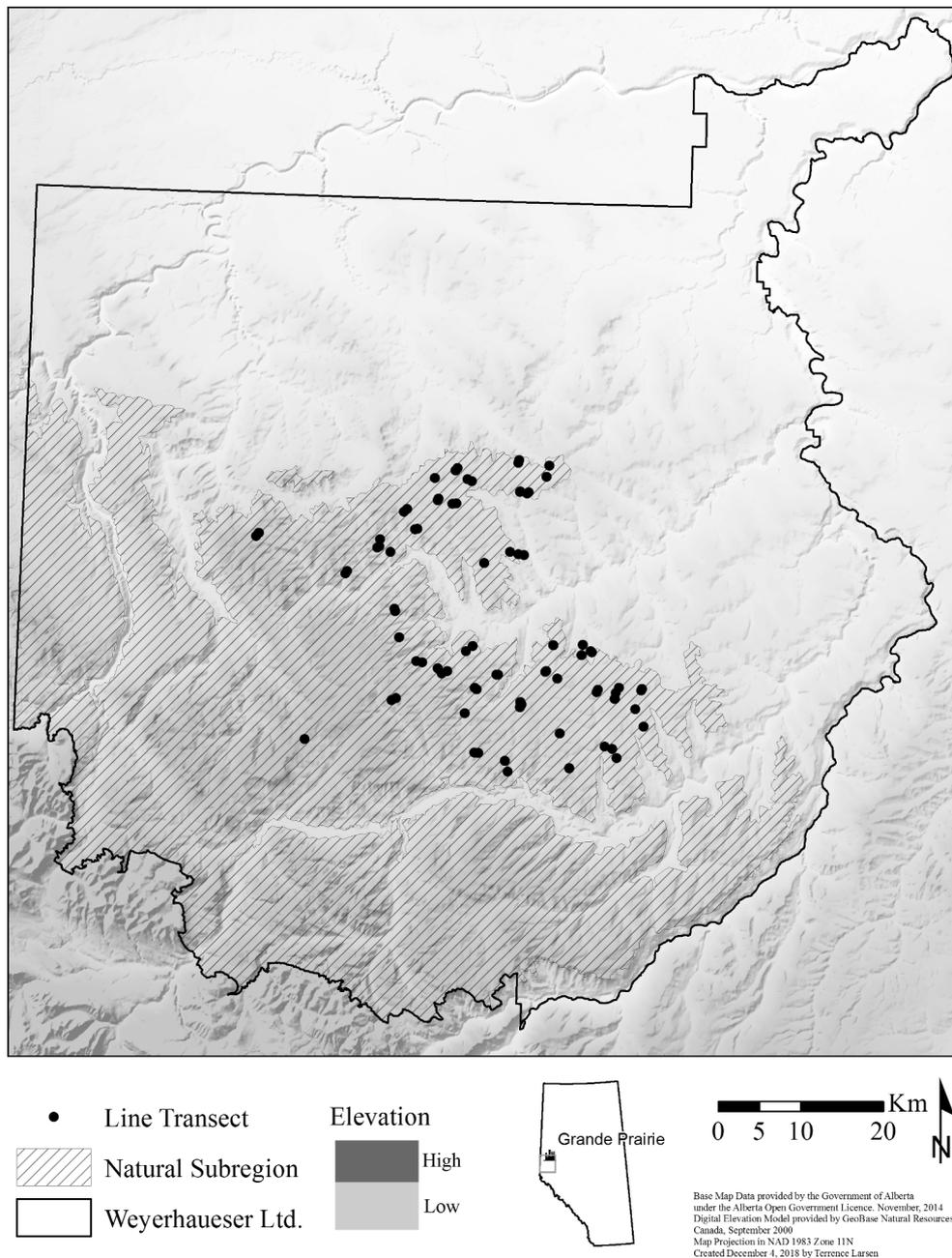


Fig. 1. Map showing the locations of plots (line transects) in part of the Subalpine and Upper Foothills Natural Subregions within Weyerhaeuser's Forest Management Agreement area in west-central Alberta, Canada.

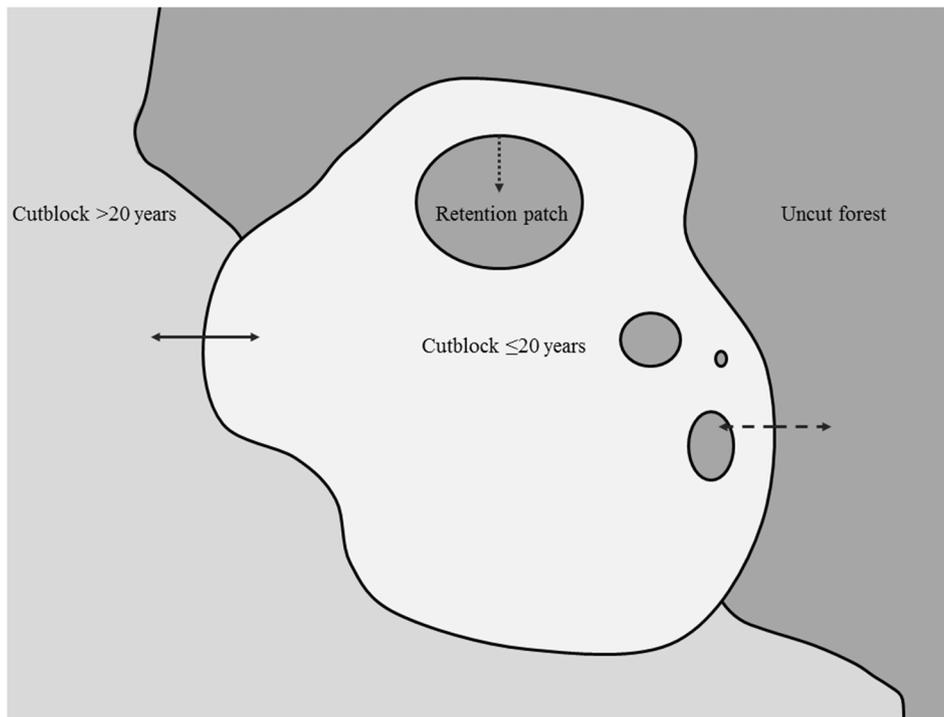
tree crowns and merged all polygons that overlapped. We defined forest edge as the continuous perimeter (polyline) of both cutblocks and retention patches.

### 2.3. Habitat stratification and vegetation sampling

We used a stratified random design to sample vegetation along different forest edge treatments. First, we stratified cutblocks by regenerating age class (3–10, 11–20, and 21–43 years) that corresponded to stages of horizontal and vertical tree development following secondary succession. These changes in stand structure influence moisture and light regimes affecting understory vegetation establishment and growth (Hart and Chen, 2006). Second, we stratified the regenerating age classes based on whether or not the adjacent forest was uncut or of a different age class. We sampled these edge type strata because forest harvesting strategies in Alberta typically create a landscape where

young ( $\leq 20$  years) cutblocks tend to be adjacent to uncut forest (1st pass edge type) or old (21–43 years) cutblocks (2nd pass edge type). Third, we further stratified retention patches by size using a cutoff value (0.5 ha) that reflected the minimum size used to define retention patches based on aerial photo interpretation techniques. Our aim was to sample 'small' and 'large' retention patches evenly as a means to capture a wide range of conditions as patches may be purposefully selected to meet a series of other management objectives. For example, patches of spruce or deciduous species may have been retained where pine forest was harvested specifically as part of mountain pine beetle (*Dendroctonus ponderosae*) control efforts. It is also possible that certain patches of trees may have been retained due to soil moisture conditions (wet areas).

We generated random locations within our forest edge strata that were  $> 120$  m from known anthropogenic features (roads, well sites, pipelines, seismic lines, or powerlines) to reduce the potential for other



**Fig. 2.** Diagram depicting vegetation transects in relation to three forest edge types: (1) young cutblock  $\leq 20$  years of age adjacent to uncut forest matrix (dash line); (2) young cutblock adjacent to old cutblock  $> 20$  years of age (solid line); and (3) uncut forest retention patch (dot line).

edge effects. To improve sample efficiency, we matched forest edge types (cutblock and retention) at the level of the cutblock and limited our sampling to accessible roads within the study area. During the summer (July to September) of 2013, we navigated to 124 random first ( $n = 72$ ) and second pass ( $n = 18$ ) edge locations, as well as 34 retention patches using a hand-held GPS unit. At each random edge location, we located the base of the nearest edge tree ( $\geq 5$  cm @ 1.3 m diameter-at-breast-height [DBH]). For cutblock edges, we then ran two opposing 60 m transects that were perpendicular to the edge, and for retention edges, we ran a single 60 m transect through the patch (Fig. 2). Along each transect, we established ten  $1 \text{ m}^2$  (0.56 m, 2.5, 5, 7.5, 10, 20...60) subplots and eight  $10 \text{ m}^2$  subplots (1.7 m, 5, 10, 20...60) (Fig. 2). We sampled more within the first 10 m of transects to capture potentially abrupt changes of plants as edge effects in the boreal forest may occur over relatively short distances (Harper and Macdonald, 2002; Harper et al., 2004; Kowal and Cartar, 2012).

We quantified plant-based food resources thought to be important to grizzly bears in west-central Alberta including sweet-vetch roots (*Hedysarum* spp.), horsetail (*Equisetum arvense*), cow parsnip (*Heracleum lanatum*), blueberry (*Vaccinium myrtilloides*), huckleberry (*V. membranaceum*), lingonberry (*V. vitis-idaea*), and buffaloberry (*Shepherdia canadensis*) (Munro et al., 2006). We also included raspberry (*Rubus idaeus*) despite it being of lower seasonal importance compared to the other species (Appendix Table A1). Raspberry tended to be less dominant in bear diets and had a lower energetic value when compared to the blueberry species (*Vaccinium* spp.) (Coogan et al., 2014; Munro et al., 2006). Our interest in raspberry was because of its potential to outcompete the blueberries. Soil disturbance associated with forest harvesting or post-harvest site preparation may promote raspberry establishment, growth, and expansion (Lautenschlager, 1997), whereas blueberries tend to thrive where the understory has not been disturbed (Martin, 1983; Moola and Mallik, 1998). Because of differences in the spatial growth pattern (i.e. distributed versus clumped) and sizes of these plant species, we used  $1\text{-m}^2$  subplots to measure sweet-vetch, horsetail, and the blueberries and  $10\text{-m}^2$  subplots to measure cow parsnip, buffaloberry, and raspberry.

For each subplot, we visually estimated the percent cover (0–100) of forbs and shrubs, and we counted fruit using a time constraint of one minute per subplot. In addition, we estimated the percent cover of other (competing) vegetation grouped as graminoids and sedges (*Carex* spp.), forbs ( $1\text{-m}^2$  subplots only), shrubs (short [ $\leq 1.5$  m] or tall [ $> 1.5$  m] shrubs), and small trees  $< 5$  cm DBH. We also located the nearest three trees and recorded the number of pine, other coniferous and deciduous species. For transect lines that traversed cutblocks, we recorded the distance from each subplot to the nearest retention tree if it was less than the subplot distance. Because subplots associated with cutblock transects could have occurred in or partially within retention patches, we recorded the forest type (cutblock or retention) based on that which represented the majority of the subplot area. We used a digital range finder ( $\pm 1$  m accuracy) to measure tree distances from each subplot. To improve our understanding of factors influencing grizzly bear food distribution/abundance along forest edges, particularly uncut forest associated with cutblock and retention patch edges, we report the proportion of pine, conifer, and deciduous tree species. Proportions were based on the total number of trees across transects.

#### 2.4. GIS variables

We used Geographic Information System (GIS) raster layers representing climate, soil moisture, and terrain as predictor variables associated with local environmental conditions (Table 1). For climate and terrain, we used a digital elevation model (DEM) – bare earth – derived from airborne Lidar and resampled the  $1 \text{ m}^2$  Lidar DEM to  $100 \text{ m}^2$  ( $10 \times 10$  m pixel) DEM using the nearest neighbors. Slope and aspect grids were created at each scale and used to calculate absolute aspect (subtract grid value from 180), which aligns the index on a north/south axis (Pierce Jr. et al., 2005). For soil moisture, we used a Wet Areas Mapping depth-to-water index that was also derived from airborne Lidar data at a  $1 \text{ m}^2$  resolution (White et al., 2012). Attributes for each of the environmental factors were extracted to subplots and treated as continuous predictors (Table 1). ArcGIS 10.1 was used to process spatial data (ESRI® Redlands, CA).

**Table 1**  
Variables used to predict the distribution and abundance of grizzly bear foods in west-central Alberta, Canada.

Factor	Code	Description	Range
Competing vegetation	Forb	Percent cover of forbs.	0–85%
	GrSd	Percent cover of graminoids and sedges.	0–100%
	ShrS	Percent cover of shrub species ( $\leq 1.5$ m).	0–100%
	ShrT	Percent cover of shrub species ( $> 1.5$ m).	0–100%
	SmlT	Percent cover of small diameter tree species ( $< 5$ cm diameter-at-breast height)	0–95%
Environmental conditions	Elev	Elevation derived from LiDAR ( $1 \times 1$ m pixel).	966–1531 m
	Wam	Wet areas mapping of depth-to-water derived from LiDAR ( $1 \times 1$ m pixel).	0–57.7
	Asp1 or Asp10	Absolute aspect ( $1 \times 1$ and $10 \times 10$ m pixel).	–180–180
Forest type	Slp1 or Slp10	Slope ( $1 \times 1$ and $10 \times 10$ m pixel).	0 - 35°
	CutY <sub>3-10</sub>	Young cutblock between 3 and 10 years of age.	
	CutY <sub>11-20</sub>	Young cutblock between 11 and 20 years of age.	
	CutY	CutY <sub>3-10</sub> grouped with CutY <sub>11-20</sub> .	
	CutO	Old cutblock between 21 and 43 years of age.	
	CutYO	CutY <sub>11-20</sub> grouped with CutO.	
	Cut	Cutblock; regenerating forest $\leq 43$ years of age.	
	Uncut	Fire origin; uncut forest $> 43$ years of age.	
	Ret	Retention (single tree or patch) of uncut forest within a cutblock.	
	Edge distance	CbEdDist	Distance to the nearest cutblock edge tree.
CbEdDist10		CbEdDist as a binary variable; 1 ( $\leq 10$ m) or 0 ( $> 10$ m).	
RetEdDist		Distance to the nearest cutblock or retention edge tree.	0.56–60 m
RetEdDist10		RetEdDist as a binary variable; 1 ( $\leq 10$ m) or 0 ( $> 10$ m).	

## 2.5. Forest types and edge distance variables

We produced a series of nominal variables to distinguish different combinations of forest types (Table 1). We started with a simple binary variable to differentiate cutblocks from uncut forest, which we assumed as fire origin. We then created additional variables to represent different age classes of cutblock and to distinguish uncut forest from retention patch. Next, we created a variable to represent distance to the edge starting point, as well as a variable to represent where edge distance was closer to a retention patch, which was only possible for cutblock transects.

## 2.6. Model fitting

We modelled the occurrence (presence/absence) and abundance (percent cover as an integer or counts of fruit) of forbs, shrubs, and fruits from shrubs using logistic regression and count models. Sweet-vetch roots and buffaloberry shrubs were too uncommon to model their distribution and abundance, but observations were sufficient for the other species inventoried. Because we considered the transect line as the sample unit, we specified transect ID as a cluster variable (robust/sandwich estimates of variance) to account for spatial dependence in our data (between cluster correlation) (Rogers, 1983). Our dependent variables showed evidence of over-dispersion (variance exceeded the mean) and zero-inflation (more zeros than what would be expected from a standard distribution) (Cox, 1983; Tu, 2002). As such, we fit four count models (poisson or negative binomial with and without zero-inflation) to identify the most appropriate model given the distribution of data. We used Stata 12.1 to fit statistical models (StataCorp., 2011).

Akaike Information Criteria (AIC), plots of observed vs. predicted values, and a Vuong test (bias correction) confirmed that zero-inflated negative binomial (ZINB) fit best in each case (Coxe et al., 2009; Desmarais et al., 2013; Perumean-Chaney et al., 2013). We concluded that ZINB was appropriate given that the relationships followed what we know from the literature (Joseph et al., 2009; Nielsen et al., 2010, 2004c). Plants are sessile, and in this study, easily identified, so we assumed that the majority of zeros were true and arise from ecological processes (Martin et al., 2005; Welsh et al., 2000). The ZINB mixture model was selected as it allows for the same or different variables to be simultaneously estimated, which may help to identify variables that influence occurrence compared to those that drive abundance (e.g., Nielsen et al., 2005).

## 2.7. Purposeful variable selection and the baseline model

For each dependent variable, we purposefully selected predictor variables (Hosmer and Lemeshow, 2005) to identify a baseline model. The baseline model consisted of variables associated with competing vegetation and environmental conditions. We also used univariate analysis and Wald tests to determine what forest type variable should be used, as well as whether or not to use the continuous or binary form of edge distance. To investigate potential non-linear responses, we considered a quadratic (squared term) effect for all continuous variables. For the inflate portion of the ZINB model, we used the best fitting logit model structure (see below). To ensure that collinearity and multicollinearity were not present in any of the fitted models, we used Pearson's correlation coefficient ( $r < 0.6$ ) and variance inflation factors ( $VIF < 3$ ) to examine variable associations (Zuur et al., 2010).

## 2.8. Model selection to evaluate support for predictions

We evaluated competing models (hypotheses) in two stages of model selection, and used small sample size AIC ( $AIC_c$ ) to identify the most parsimonious model (Anderson et al., 2000). When the change in the  $AIC_c$  value was less than two units amongst the models considered, we chose the model with the fewest parameters ( $k$ ) as the best fitting model.  $AIC_c$  weights ( $w_i$ ) were used to evaluate the strength of support for a particular model; weights of  $\geq 0.9$  can be interpreted as the probability that a single model would be supported over others in the candidate set (Anderson and Burnham, 2002). However, we did not dismiss uninformative model parameters and therefore model weights should be interpreted cautiously (Arnold, 2010).

In stage one, we considered four *a priori* models including a null (intercept) model that assumed no spatial pattern, a baseline model containing variables related to competing vegetation and environmental conditions, and separate models to evaluate the effect of forest type considering retention as a unique category (Table 2). In stage two, we considered five *a priori* models including a baseline null model (best fitting model from stage one), a model that represented cutblock edge distance, a model that considered edge distance where retention was the nearest edge tree, as well as models that considered an interaction (multiplicative effect) between forest type (with or without retention) and the two edge distance variables (Table 2). It was possible that the interaction between edge distance and forest type with retention fit better, even if retention was not considered in the baseline null model.

**Table 2**

Models (hypotheses) used to test the predictions that forest type and habitat edge distance influenced the distribution and abundance of grizzly bear foods. For each stage of analysis, the baseline null model may or may not be included in subsequent models.

Analysis stage	Model number	Name	Description
One	1	Null	No spatial pattern.
	2	Baseline null	Competing vegetation and/or environmental conditions explained spatial variation.
	3	Forest type	Forest type explained spatial variation.
	4	Forest type with retention	Retention distinguished as an additional forest type explained spatial variation.
Two	5	Baseline null	Best fitting model from analysis stage one.
	6	Cutblock edge distance	Distance to the nearest cutblock edge tree explained spatial variation.
	7	Cutblock or retention edge distance	Distance to the nearest cutblock or retention edge tree explained spatial variation.
	8	Cutblock edge distance interaction	The multiplicative effect of forest type and the distance to the nearest cutblock edge tree explained spatial variation.
	9	Cutblock or retention edge distance interaction	The multiplicative effect of forest type and the distance to the nearest cutblock or retention edge tree explained spatial variation.

for stage one. As such, we retained the best fitting variable as the baseline null model. We report marginal estimates by forest type and edge distance based on the best fitting models determined from stage one and two of the analysis. For estimation, predictor variables associated with competing vegetation were set to zero, otherwise, all other predictors were set to their mean value.

### 2.9. Model evaluation

Sample size was insufficient to split the data into training and testing data sets, so we used a cross-validation method to evaluate the predictive performance of the best fitting AIC<sub>c</sub>-selected models. For each model, we ran *k*-fold cross-validation with 10 data partitions. We repeated this 10 times to calculate the average root mean square error (RMSE), mean absolute error (MAE), and Efron's pseudo-R<sup>2</sup>. For the logit models, we also used 10-fold cross-validation repeated 10 times to calculate the area under the receiver operating curve (ROC) and to derive measures of classification accuracy that included the percent of correctly classified occurrences, the false positive rate, the false negative rate, and the percent deviation from known occurrence (e.g. Fielding & Bell 1997; Knopff et al. 2009). Presence was determined as the optimal cutoff probability where sensitivity 'crossed' specificity (Hosmer and Lemeshow, 2005). For count models, we calculated Pearson's correlation coefficient, Spearman's rank correlation coefficient, and fit a linear regression model (bias and spread) to the observed and predicted values (Potts and Elith, 2006). Although we assessed each model based on statistical fit, we also considered the ecological plausibility of the coefficients estimated.

## 3. Results

### 3.1. Retention patch size and tree species composition

We sampled plants along forest edges and retention patches that ranged in size from 0.01 to 7.50 ha ( $\bar{x}$  = 1.16, SD = 1.80). When we included an additional nine retention patches that were sampled by chance in cutblocks, patch size ranged from < 0.01 to 7.50 ha ( $\bar{x}$  = 1.09, SD = 1.89). Each transect consisted of ten 1-m<sup>2</sup> and eight 10-m<sup>2</sup> subplots yielding 1240 and 992 observations for model estimation, respectively. Tree species composition differed between uncut and retention forest types. We found more pine and less deciduous tree species associated with uncut forests (pine = 40% and deciduous = 6%) compared to retention patches (pine = 20% and deciduous = 26%). The proportion of black spruce (uncut = 40% and retention = 34%) and other coniferous species (uncut = 34% and retention = 19%) were more similar between forest types, however.

### 3.2. The effect of forest type on food distribution and abundance

Here we tested whether forest type with or without retention best

predicted the distribution/abundance of grizzly bear foods. Model selection revealed that there were only two instances where the null model (no spatial pattern) was selected over models containing some variant of forest type. In general, grizzly bear foods were most common and abundant in young cutblocks and comparably low in both old cutblocks and uncut forests. However, huckleberry and lingonberry were equivalent to or higher in uncut forests compared to young cutblocks. For the six species, model selection revealed strong support ( $w_i$  = 0.95–1.00) for retention being included as an additional predictor (Table 3). On average, horsetail was 1.77 and raspberry was 2.5 times more likely to occur in retention than in uncut forests, and horsetail was 2.29 times more abundant in retention (Table 4.). Conversely, huckleberry, blueberry, and lingonberry shrubs were 1.59, 2.25, and 1.42 times more likely to occur in uncut forests than retention, respectively (Table 4).

### 3.3. The effect of edge distance on food distribution and abundance

Model selection revealed that each of the species considered in our study were influenced by the effect of edge distance, and with the exception of lingonberry, edge distance responses also varied by forest type (Table 5). In young cutblocks, horsetail occurrence was positively related to an increase in edge distance, whereas the relationship with edge distance was negative for old cutblocks, uncut forests, and retention patches (Fig. 3). Cow parsnip was more likely to occur as edge distance increased, and in general, was more abundant further from edges with the exception of the youngest cutblock age class (3–10 years) and in retention patches (Fig. 3). In young cutblocks, cow parsnip was 4.25 times more abundant near (72% cover) than far (17% cover) from edges (Fig. 3).

Raspberry shrubs tended to be more abundant further than 10 m from edge, yet fruit was 1.93 times more abundant near (count = 2.81) than far away (count = 1.45) from an edge. Huckleberry was positively associated with edge and especially in uncut forests (Fig. 4). In uncut forests, huckleberry shrubs and fruits were 1.61 and 1.98 times more likely to occur near (shrub = 42% and fruit 11%) than far (shrub 26% and fruit 5%) from a forest edge, respectively. Blueberry was also positively associated with forest edge, particularly in young cutblocks with shrub occurrence decreasing with edge distance in all forest types except old cutblocks (Fig. 5). The effect of edge distance on blueberry was most pronounced in retention patches, as shrub occurrence decreased precipitously within 10 m of the retention edge (Fig. 5). Blueberry fruit was more likely to occur near forest edges irrespective of forest type (Fig. 5). For lingonberry, the effect of edge distance consistently increased with distance, whereas lingonberry shrub occurrence, abundance, and fruit occurrence decreased with distance from edge (Fig. 5).

Finally, model selection revealed that for each species, the best fitting edge distance variable was not always consistent between logistic and count models (Table 6). However, model selection also

**Table 3**

Summary of the best fitting models from analysis stage one that described the distribution and abundance of grizzly bear foods. Model log-likelihood (LL), number of estimated parameters (*k*), small sample size corrected Akaike's Information Criterion (AIC<sub>c</sub>), AIC<sub>c</sub> difference (ΔAIC<sub>c</sub>), and Akaike weight (*w<sub>i</sub>*) are shown.

Model	Type	Species	Name	LL	<i>k</i>	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	<i>w<sub>i</sub></i>	
Logit	Forb	Horsetail	Forest type with retention	-766.1	10	1554.1	0.0	1.00	
		Cow parsnip	Baseline null	-413.8	8	844.9	0.0	0.49	
	Shrub	Huckleberry	Forest type with retention	-595.9	9	1211.5	0.0	0.95	
		Blueberry	Forest type with retention	-481.3	10	984.5	0.0	0.99	
		Ligonberry	Forest type with retention	-655.9	13	1341.2	0.0	0.99	
		Raspberry	Forest type with retention	-392.4	11	809.2	0.0	0.96	
	Fruit	Huckleberry	Forest type	-222.7	7	460.5	0.0	0.56	
		Blueberry	Forest type	-310.6	9	640.8	0.1	0.49	
		Ligonberry	Forest type	-355.4	8	728.0	0.0	0.72	
		Raspberry	Forest type	-187.8	8	392.8	0.0	0.52	
		ZINB	Forb	Horsetail	Forest type with retention	-2519.3	22	5092.7	0.0
	ZINB	Forb	Cow parsnip	Forest type	-871.2	17	1782.1	0.0	0.75
Huckleberry			Forest type	-1380.2	19	2805.7	0.0	0.75	
ZINB	Shrub	Blueberry	Forest type	-1294.4	22	2642.8	0.0	0.48	
		Ligonberry	Forest type	-1716.5	19	3478.4	0.0	0.76	
		Raspberry	Forest type	-898.3	19	1841.9	0.0	0.64	
	Fruit	Huckleberry	Forest type	-407.9	12	842.6	0.0	0.52	
		Blueberry	Forest type	-856.3	20	1760.8	0.0	0.74	
		Ligonberry	Baseline null	-810.3	14	1652.5	0.0	0.49	
		Raspberry	Forest type	-417.5	14	866.8	0.0	0.71	

illustrated that for all species with the exception huckleberry, an edge distance variable that accounted for instances in cutblocks where retention edges were closer than starting point edges, fit better (Table 6). See the appendix for model AIC<sub>c</sub> scores (Tables A2-A3), model coefficient estimates (Tables A6-A11), and model evaluation statistics (Tables A12-A14).

**4. Discussion**

Understanding how forest disturbances influence grizzly bear food supply is an essential component of managing habitat in support of conservation and recovery of this threatened species in Alberta (Nielsen et al., 2017). This research provides the first quantitative assessment of grizzly bear food distribution/abundance in relation to forestry cutblock edges and undisturbed remnant forest within cutblocks. Our results support our prediction that grizzly bear food supply would be greater near forest edges, and that retention patches and uncut forest matrix would be similar relative to edge distance responses. Positive

edge effects were associated with more shrubs and increased fruit production of the three blueberry species we measured in this study, which are known to be sensitive to ground disturbance (Martin, 1983; Moola and Mallik, 1998; Nielsen et al., 2004b; Dawe et al., 2017;). Positive effects of certain forest edges were also associated with horsetail and cow parsnip. However, these species, which are known to respond positively to ground disturbance (Bartos and Mueggler, 1982; Lautenschlager, 1997; Nielsen et al., 2004c), were generally more common/abundant within cutblocks and away from edges. We accept our prediction that edge distance responses would be similar between edge types (cutblock-uncut and cutblock-retention), but we reject our prediction that food supply would not differ between forest types (uncut and retention). For example, the relationship between blueberry shrub occurrence and edge distance was negative both in uncut and retention forest types, yet shrub occurrence was much lower in retention overall. Collectively, these findings suggest that forest harvesting strategies that create forest edges, such as those associated with natural disturbance, could improve grizzly bear habitat conditions. However,

**Table 4**

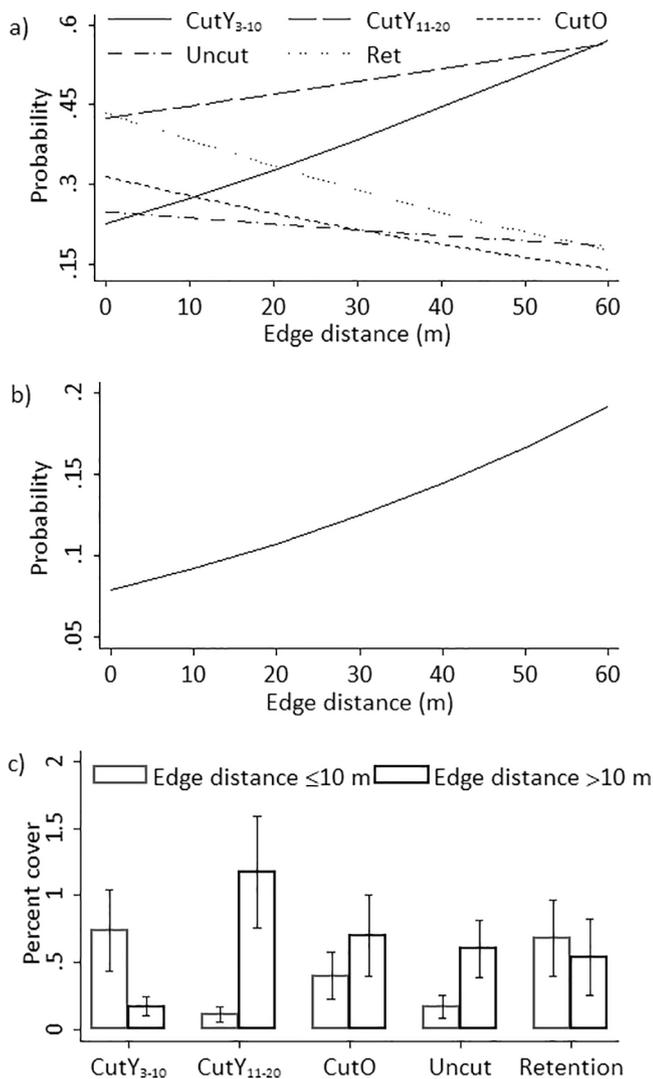
Marginal estimates (mean and standard error) from the best fitting logistic regression or zero inflated negative binomial models from analysis stage one that described the distribution (probability of occurrence) and abundance (count) of grizzly bear foods by forest type.

Model	Species	Type	CutY <sub>3-10</sub>	CutY <sub>11-20</sub>	CutY	CutO	CutYO	Cut	Uncut	Ret	
Logit	Horsetail	Forb	0.30 (0.08)	0.47 (0.08)		0.24 (0.08)			0.22 (0.05)	0.39 (0.07)	
	Cow Parsnip										
	Huckleberry	Shrub			0.44 (0.05)	0.30 (0.09)			0.35 (0.06)	0.22 (0.05)	
		Fruit			0.09 (0.04)	0.02 (0.02)			0.10 (0.03)		
	Blueberry	Shrub			0.39 (0.07)	0.27 (0.10)			0.27 (0.07)	0.12 (0.05)	
		Fruit	0.37 (0.08)	0.22 (0.08)		0.09 (0.05)			0.10 (0.03)		
	Ligonberry	Shrub	0.30 (0.06)	0.50 (0.11)		0.37 (0.08)			0.51 (0.07)	0.36 (0.08)	
		Fruit			0.23 (0.05)	0.04 (0.04)			0.21 (0.04)		
	Raspberry	Shrub			0.43 (0.07)	0.11 (0.04)			0.06 (0.02)	0.15 (0.05)	
		Fruit			0.20 (0.05)	0.03 (0.02)			0.03 (0.01)		
	Count	Horsetail	Forb			2.00 (0.43)	1.19 (0.32)			1.65 (0.51)	3.78 (0.94)
		Cow Parsnip		0.28 (0.12)	0.82 (0.29)		0.53 (0.24)			0.49 (0.18)	
Huckleberry		Shrub						2.29 (0.39)	3.79 (0.85)		
		Fruit						0.31 (0.12)	0.78 (0.29)		
Blueberry		Shrub	10.66 (2.30)				6.82 (1.81)		6.20 (1.71)		
		Fruit	23.76 (8.62)				9.54 (2.86)		9.50 (3.02)		
Ligonberry		Shrub			2.05 (0.37)	1.04 (0.26)			2.65 (0.40)		
		Fruit									
Raspberry		Shrub			1.97 (0.58)	0.49 (0.19)			0.72 (0.29)		
		Fruit			1.75 (0.43)	0.89 (0.26)			0.90 (0.31)		

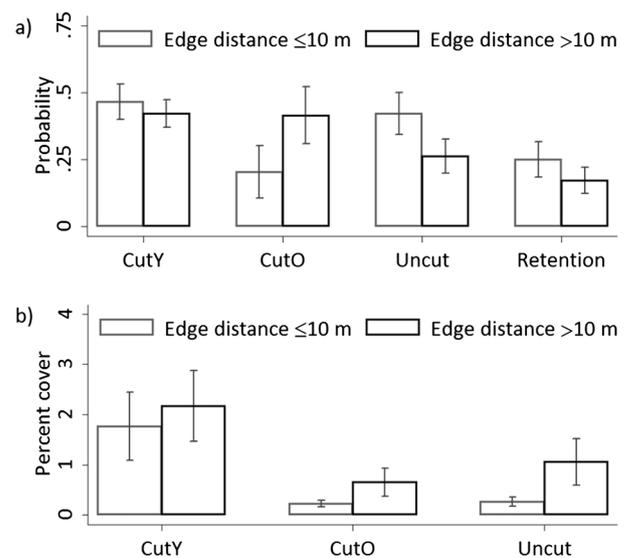
**Table 5**

Summary of the best fitting models from analysis stage two that described the distribution and abundance of grizzly bear foods. Model log-likelihood (LL), number of estimated parameters (*k*), small sample size corrected Akaike's Information Criterion (AIC<sub>c</sub>), AIC<sub>c</sub> difference (ΔAIC<sub>c</sub>), and Akaike weight (*w<sub>i</sub>*) are shown.

Model	Type	Species	Name	LL	<i>k</i>	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	<i>w<sub>i</sub></i>
Logit	Forb	Horsetail	Cutblock or retention edge distance interaction	-758.1	15	1550.7	0.0	0.73
		Cow parsnip	Cutblock or retention edge distance	-407.1	9	833.7	0.0	0.85
	Shrub	Huckleberry	Cutblock edge distance interaction	-588.1	13	1205.6	0.0	0.51
		Blueberry	Cutblock or retention edge distance interaction	-472.0	14	975.9	0.0	0.92
		Ligonberry	Cutblock or retention edge distance	-649.2	14	1330.3	0.0	0.74
		Raspberry	Baseline null	-392.4	11	809.3	0.0	0.30
	Fruit	Huckleberry	Cutblock edge distance	-219.0	8	455.2	0.0	0.52
		Blueberry	Cutblock edge distance	-304.7	10	631.3	0.0	0.66
		Ligonberry	Cutblock or retention edge distance	-346.8	9	713.2	0.0	0.68
		Raspberry	Baseline null	-187.8	8	392.8	0.0	0.31
ZINB	Forb	Horsetail	Baseline null	-2519.3	22	5092.7	0.0	0.66
		Cow parsnip	Cutblock edge distance interaction	-851.8	23	1760.7	0.0	0.90
	Shrub	Huckleberry	Baseline null	-1380.2	19	2805.7	0.0	0.45
		Blueberry	Baseline null	-1294.4	22	2642.8	0.0	0.46
		Ligonberry	Cutblock or retention edge distance	-1712.9	20	3473.9	0.0	0.60
		Raspberry	Cutblock or retention edge distance interaction	-894.3	20	1836.7	0.8	0.29
	Fruit	Huckleberry	Baseline null	-407.9	12	842.6	0.9	0.24
		Blueberry	Baseline null	-856.3	20	1760.8	0.0	0.59
		Ligonberry	Baseline null	-810.3	14	1652.5	0.0	0.54
		Raspberry	Cutblock or retention edge distance	-413.2	15	860.9	0.0	0.61



**Fig. 3.** Marginal estimates (mean and standard error) from fitted logistic regression models that described the effect of edge distance on the probability of occurrence of horsetail by forest type (a) and the probability of occurrence (b) and percent cover (c) of cow parsnip.



**Fig. 4.** Marginal estimates (mean and standard error) from fitted logistic regression or zero-inflated negative binomial regression models that described the effect of edge distance on the probability of occurrence of huckleberry shrubs (a) and the percent cover of raspberry shrubs (b).

we suspect that grizzly bear habitat could be improved further if efforts were made to enhance critical food resources like fruit (Braid et al., 2016), especially in remnant forest patches.

Our finding that blueberry species were positively associated with forest edges was consistent with other research that has suggested mechanical damage to rhizomes following harvest and post-harvest site preparation (e.g. scarification) would negatively impact shrub populations (Haeussler et al., 1999; Martin, 1983; Minore, 1984; Nielsen et al., 2004c). For huckleberry, the result may be delayed vegetative recovery, and to the point, where fruit production would then be inhibited by tree growth and shading (Martin, 1983; Minore, 1984). Conversely, blueberry and lingonberry shrubs may recover more quickly after a disturbance, which may explain why fruit production can occur away from edges and in early seral forests under open canopy conditions (Moola and Mallik, 1998; Nielsen et al., 2004c; Dawe et al., 2017). Yet, blueberry shrubs and fruit were more common at forest edges where disturbance to the understory was likely to be less. This finding

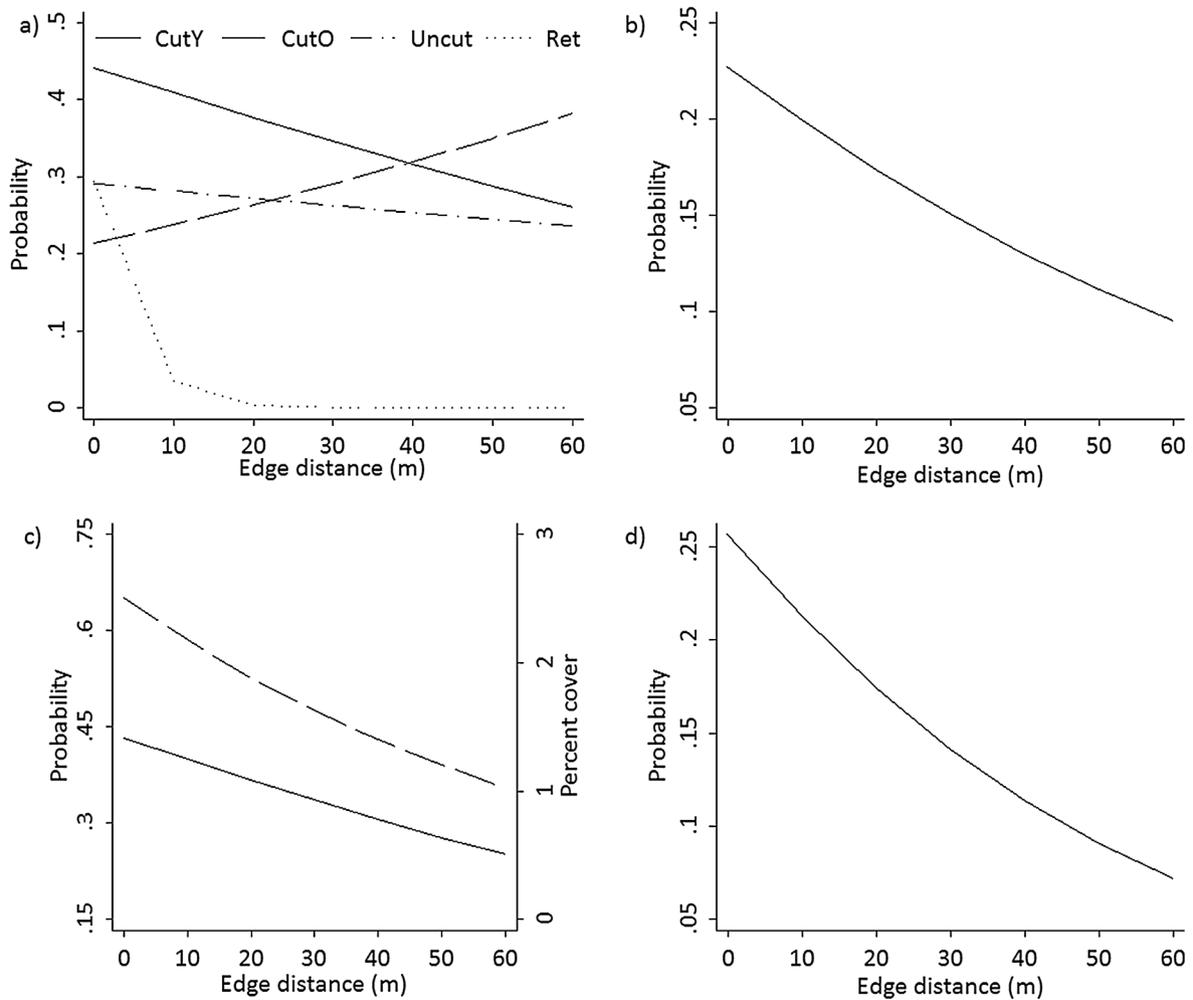


Fig. 5. Marginal estimates (mean) from fitted logistic regression or zero-inflated negative binomial regression models that described the effect of edge distance on the probability of occurrence of blueberry shrub by forest type (a) and the probability of occurrence of fruit (b), as well as the probability of occurrence (solid line) and percent cover (dashed line) of lingonberry shrub (c), and the probability of occurrence of lingonberry fruit (d).

Table 6

Summary of the best fitting models from analysis stage two that described the edge distance responses of grizzly bear foods by forest type. Symbols refer to higher (+), lower (-), or no difference (nd) in the distribution (probability of occurrence) or abundance (count) of food near habitat edge.

Model	Type	Species	Distance variable type	Distance variable response	Forest type distance variable response						
					Cut <sub>3-10</sub>	Cut <sub>11-20</sub>	CutY	CutO	Uncut	Ret	
Logit	Forb	Horsetail	RetEdDist		-	-		+	+	+	
		Cow parsnip	RetEdDist	-							
	Shrub	Huckleberry	CbEdDist10					nd	-	+	nd
		Blueberry	RetEdDist				+	-	+	+	
		Ligonberry	RetEdDist	+							
	Fruit	Raspberry									
		Huckleberry	CbEdDist10	+							
		Blueberry	CbEdDist	+							
		Ligonberry	RetEdDist	+							
ZINB	Forb	Raspberry									
		Horsetail									
	Shrub	Cow parsnip	CbEdDist10		+	-		nd	-	nd	
		Huckleberry									
	Fruit	Blueberry	RetEdDist	+							
		Ligonberry	RetEdDist	+							
		Raspberry	CbEdDist10				nd	-	-		
		Huckleberry									
		Raspberry	RetEdDist10	+							

corresponded with research from Ontario, Canada, that showed partial tree removal (shelterwood) resulted in abundant blueberry shrubs and fruits compared to cutblocks with full tree removal (Moola and Mallik, 1998). Consistent with our findings, Nielsen et al (2004b) showed that lingonberry shrubs may respond positively to scarification, yet fruit production was still highest in uncut forest. Increased fruit production at edges for all blueberry species can likely be explained by increased light availability for shrubs that have not suffered mechanical damage. The management challenge is that as part of silviculture prescriptions, soil disturbance is necessary to create microsites for pioneer tree species such as pine to establish and grow. As we and others have showed, this can negatively affect understory plants depending on the timing (i.e. summer vs. winter) and intensity of the disturbance (Berger et al., 2004; Coxson and Marsh, 2001). Often, plants that respond well to disturbance, and that are able to quickly invade and colonize microsites such as horsetail, cow parsnip, and raspberry, tend to be prolific.

Edge effects in forested landscapes can vary from less than ten meters to more than a few hundred meters (Baker et al., 2013; Dabros et al., 2017; Harper et al., 2015, 2004; Kowal and Cartar, 2012). We found that edge responses were generally linear in shape rather than having abrupt transitions. We suspect that variation in the distribution/abundance of plant communities along the edge distance gradient could be attributed to variation in, and changes to, local effects that include: environmental conditions (e.g. light, moisture, and temperature); stand composition (i.e. tree species and stand age) and structure (i.e. tree mortality and windthrow); understory vegetation responses from other competing species; soil disturbance from harvest or site preparation; and even herbivory (Dabros et al., 2017; Harper and Macdonald, 2002; Harper et al., 2015, 2004). Our results also demonstrated that edge effects can be long lasting. For example, as young cutblocks aged and the occurrence probability of horsetail declined, the occurrence of horsetail along older cutblock edges.

The majority of previous research on forest structural retention and understory vegetation have focused on community level changes in diversity in relation to the amount of retention (Aubry et al., 2009; Bradbury, 2004; Craig and Macdonald, 2009; MacDonald and Fenniak, 2007) rather than species-specific responses. We showed that of the six species measured in our study, only two increased (horsetail and raspberry), one showed no difference (cow parsnip), and the remaining three (blueberries) were reduced in retention patches compared to uncut forest. This was consistent with the findings of Bradbury (2004) that showed marked differences in plant communities when retention patches were compared to the pre-harvest forest. The author attributed these differences to retention patch size with smaller patches having microclimatic conditions more similar to cutblocks, whereas large patches would be more similar to the forest matrix (Bradbury, 2004). Given that we sampled a wide range of retention patch sizes, we suspect that other factors were responsible. For instance, we showed that retention patches tended to have less pine and more deciduous tree species compared to the uncut forest matrix. This is consistent with other studies that showed differences in understory plant composition between conifer versus deciduous-dominated stands (Hart and Chen, 2006; Kembel et al., 2006; Légaré et al., 2001; MacDonald and Fenniak, 2007). Conifer forests are less productive with fewer understory competitors and therefore can be dominated by ericaceous species such as blueberries, especially in pine cover types (Hart and Chen, 2006; Ihalainen and Pukkala, 2001; Kembel et al., 2006; Légaré et al., 2001; MacDonald and Fenniak, 2007; Strong, 2011).

We suspected that the observed difference in forest tree composition could be associated with how retention patches were selected. Forest companies have been known to favor the retention of deciduous tree species because conifers are more susceptible to windthrow (Work et al., 2003). In our study area, forest operators follow planning standards and general guidelines (operational ground rules) regarding structure retention, however, strategies may differ between companies. In general, the aim is to: 1) resemble the previous forest; 2) leave larger

patches rather than smaller ones; 3) maintain as much individual stems of non-merchantable trees as possible; 4) allow for connectivity between undisturbed forests at the cutblock boundary as well as riparian buffers; 5) minimize blowdown; and 6) protect ephemeral draws and intermittent streams. However, these guidelines were modified as part of targeted management directives to meet the operational requirements of the provincial mountain pine beetle strategy. In this case, mature pine was discouraged from being left behind as structural retention, but this approach has not been followed more recently as part of general retention strategies (Personal Communication John Stadt). Our results support the contention that if pine was retained in remnant forest patches, the occurrence/abundance of blueberry species could be increased. At the provincial level, forest companies strive to retain 1-5% of merchantable forest within their operational landbase, and as high as 15% has been reported (Personal Communication John Stadt). Typically, forest companies strive to retain 2.5% coniferous species and 3% deciduous species of merchantable forest within their operational land base. However, the amount of structure retention at the block level can vary between none to over 30%. A new provincial policy is currently being considered whereby a minimum of 5% would be retained as either islands or dispersed trees in each harvest block (Personal communication John Stadt). This retention amount has the potential to dramatically improve grizzly bear habitat and therefore strategies should be developed to enhance plant-based food resources such as fruit.

Previous research has demonstrated a clear link between grizzly bear use of early seral or open habitats associated with forest disturbances, and the increased availability of plant-based food resources (Hamer and Herrero, 1987a, 1987b; McLellan and Hovey, 2001; Nielsen et al., 2004a, 2004c; Serrouya et al., 2011; Waller and Mace, 1997; Zager et al., 1983). Our study confirms this finding and also provides quantitative evidence to support the view that grizzly bears are often attracted to forest edges (Blanchard, 1983; Mattson, 1997; Mattson et al., 2002; May et al., 2008), particularly the edges of forestry cutblocks (Ciarniello et al., 2015; Nielsen et al., 2004a; Wulder et al., 2013), because of increased food supply (Nielsen et al., 2008). Our finding that more horsetail and fruit at cutblock edges corresponded with previous research in the study area that showed strong selection of these habitats by female grizzly bears in the spring and fall (Stewart et al., 2013b). It has long been known, or assumed, that fall fruit availability is critical for females to build fat reserves necessary for reproduction (López-Alfaro et al., 2013; Robbins et al., 2012), which may influence local bear population density (Nielsen et al., 2017). However, it is increasingly apparent that spring protein may be more important than previously thought (López-Alfaro et al., 2015). Collectively, these findings support forest management strategies that improve both spring and fall habitat conditions for bears by increased plant-based food resource supply.

Nielsen et al (2008) used a late summer-fall grizzly bear habitat model to project changes in habitat-based carrying capacity following two different forest harvesting strategies. Overall, habitat conditions were expected to improve dramatically following timber harvest due to an increase in early seral and edge habitat (Nielsen et al., 2008). However, fewer but larger cutblocks associated with natural disturbance, compared to more and smaller cutblocks under the traditional two-pass system, resulted in less forest edge and therefore less gains in grizzly bear habitat quality (Nielsen et al., 2008; Work et al., 2003). Given that remnant forest patches produced similar edge distance effects as what was observed at the boundary of cutblocks, depending on the level of structure retained in harvest blocks, grizzly bear habitat could be enhanced beyond what was previously projected. In addition, natural disturbance forestry, which creates isolated large cutblocks, was expected to produce fewer roads and less human activity, and as a result, support more grizzly bears (Nielsen et al., 2008). Improving habitat productivity through increased food supply is a potential management strategy that could more rapidly increase the grizzly bear

population (Braid et al., 2016). This approach could help offset the demographic consequences of reduced grizzly bear survival associated with anthropogenic land activities (Boulanger and Stenhouse, 2014), which if uncontrolled are likely to hamper recovery efforts.

### 5. Conclusion

Food supply is an essential component of maintaining and enhancing grizzly bear habitat as part of provincial recovery efforts. As such, forest management activities that increase the amount of forest edges can increase food supply for bears. Our study provided evidence that understory disturbance coupled with alterations to light regimes were likely key factors that influenced the distribution/abundance of a critical grizzly bear foods such as fruit. Because blueberry shrubs, and consequently fruit, were not common in retention patches, research is needed to identify possible mechanisms. From a management perspective, positioning cutblock edges and retention patches where blueberry shrubs are more common/abundant would likely increase fruit production. However, if this was not operationally feasible, reducing soil disturbance, particularly away from edges, may be a suitable alternative approach (Berger et al., 2004).

Increasing the complexity of harvest boundaries and creating more and smaller retention patches would increase forest edges (Nielsen et al., 2004a). However, managers should also consider that remnant forest patches retained as structure retention may provide other re-

source values to bears such as security or thermal cover (Cristescu et al., 2013; Munro et al., 2006; Pigeon et al., 2016; Serrouya et al., 2011), which patch size and configuration are likely to influence. These patches may even promote landscape level connectivity as harvest area is likely to increase over time (Work et al., 2003). Future research should investigate grizzly bear use of, and response to, forest edges and retention patches to help inform management decisions. Our research lends support to the idea that natural disturbance-based forestry can improve habitat for grizzly bear because increased food supply. However, because of the strong and negative relationship between grizzly bear survival and road density (Boulanger and Stenhouse, 2014), the conservation benefits of increased food supply associated with forest harvesting can only be realized where human-access is managed appropriately.

### Acknowledgements

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### Appendix

(See Tables A1-A17)

**Table A1**  
Grizzly bear food items and their relative seasonal importance value to bears in west-central Alberta, Canada.

Common name	Species name	Seasonal importance
Horsetail	<i>Equisetum arvense</i>	High
Cow parsnip	<i>Heracleum lanatum</i>	High
Blueberry	<i>Vaccinium myrtilloides</i>	High
Huckleberry	<i>Vaccinium membranaceum</i>	High
Ligonberry	<i>Vaccinium vitis-idaea</i>	Moderate
Raspberry	<i>Rubus idaeus</i>	Low

**Table A2**  
Model log-likelihood (LL), number of estimated parameters (*k*), small sample size corrected Akaike’s Information Criterion (AIC<sub>c</sub>), AIC<sub>c</sub> difference (ΔAIC<sub>c</sub>), and Akaike weight (*w<sub>i</sub>*) from stage one logistic regression models that explained variation in the probability of occurrence of grizzly bear foods.

Type	Species	Model name	LL	<i>k</i>	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	<i>w<sub>i</sub></i>
Forb	Horsetail	Null	-858.5	1	1719.0	164.9	0.00
		Baseline null	-788.3	6	1589.4	35.3	0.00
		Forest type	-776.6	9	1572.9	18.8	0.00
		Forest type with retention	-766.1	10	1554.1	0.0	1.00
	Cow parsnip	Null	-486.0	1	974.0	129.1	0.00
		Baseline null	-413.8	8	844.9	0.0	0.49
		Forest type	-411.9	10	845.7	0.8	0.33
		Forest type with retention	-411.3	11	846.9	2.0	0.18
Shrub	Huckleberry	Null	-663.6	1	1329.2	117.7	0.00
		Baseline null	-608.6	6	1229.9	18.5	0.00
		Forest type	-600.1	8	1217.5	6.1	0.05
		Forest type with retention	-595.9	9	1211.5	0.0	0.95
	Blueberry	Null	-587.2	1	1176.5	192.0	0.00
		Baseline null	-499.0	7	1013.1	28.5	0.00
		Forest type	-487.7	9	995.1	10.5	0.01
		Forest type with retention	-481.3	10	984.5	0.0	0.99

(continued on next page)

**Table A2** (continued)

Type	Species	Model name	LL	k	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	w <sub>i</sub>
Fruit	Lingonberry	Null	-796.5	1	1595.0	253.8	0.00
		Baseline null	-669.6	9	1358.8	17.6	0.00
		Forest type	-661.4	12	1349.6	8.5	0.01
		Forest type with retention	-655.9	13	1341.2	0.0	0.99
	Raspberry	Null	-523.7	1	1049.3	240.1	0.00
		Baseline null	-453.1	8	923.4	114.1	0.00
		Forest type	-396.9	10	815.7	6.5	0.04
		Forest type with retention	-392.4	11	809.2	0.0	0.96
	Huckleberry	Null	-252.014	1	506.1	45.6	0.00
		Baseline null	-227.259	5	465.0	4.6	0.06
		Forest type	-222.742	7	460.5	0.0	0.56
		Forest type with retention	-221.974	8	461.2	0.8	0.38
	Blueberry	Null	-387.499	1	777.0	136.3	0.00
		Baseline null	-334.988	6	682.7	41.9	0.00
		Forest type	-310.615	9	640.8	0.1	0.49
		Forest type with retention	-309.401	10	640.7	0.0	0.51
	Lingonberry	Null	-418.268	1	838.6	110.6	0.00
		Baseline null	-363.837	6	740.4	12.4	0.00
		Forest type	-355.368	8	728.0	0.0	0.72
		Forest type with retention	-355.175	9	729.9	1.9	0.27
	Raspberry	Null	-242.619	1	487.3	94.5	0.00
		Baseline null	-215.729	6	444.2	51.4	0.00
		Forest type	-187.775	8	392.8	0.0	0.52
		Forest type with retention	-186.674	9	392.9	0.1	0.48

**Table A3**

Model log-likelihood (LL), number of estimated parameters (k), small sample size corrected Akaike’s Information Criterion (AIC<sub>c</sub>), AIC<sub>c</sub> difference (ΔAIC<sub>c</sub>), and Akaike weight (w<sub>i</sub>) from stage one zero-inflated negative binomial models that explained variation in the abundance of grizzly bear foods..

Type	Species	Model name	LL	k	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	w <sub>i</sub>
Forbs	Horsetail	Null	-2558.3	17	5156.4	63.7	0.00
		Baseline null	-2543.8	19	5132.8	40.1	0.00
		Forest type	-2533.6	21	5118.3	25.6	0.00
		Forest type with retention	-2519.3	22	5092.7	0.0	1.00
	Cow parsnip	Null	-890.7	11	1805.8	23.7	0.00
		Baseline null	-877.1	14	1786.0	3.9	0.11
		Forest type	-871.2	17	1782.1	0.0	0.75
		Forest type with retention	-871.5	18	1785.5	3.3	0.14
Shrubs	Huckleberry	Null	-1393.6	15	2821.6	15.9	0.00
		Baseline null	-1385.5	18	2813.4	7.8	0.02
		Forest type	-1380.2	19	2805.7	0.0	0.75
		Forest type with retention	-1379.9	20	2807.9	2.3	0.24
	Blueberry	Null	-1317.0	16	2671.0	28.2	0.00
		Baseline null	-1300.0	20	2648.1	5.3	0.03
		Forest type	-1294.4	22	2642.8	0.0	0.48
		Forest type with retention	-1292.9	23	2642.8	0.0	0.48
	Lingonberry	Null	-1730.4	16	3498.0	19.6	0.00
		Baseline null	-1726.8	17	3493.4	15.0	0.00
		Forest type	-1716.5	19	3478.4	0.0	0.76
		Forest type with retention	-1716.3	20	3480.7	2.3	0.24
Raspberry	Null	-940.4	13	1910.2	68.2	0.00	
	Baseline null	-908.7	17	1857.2	15.3	0.00	
	Forest type	-898.3	19	1841.9	0.0	0.64	
	Forest type with retention	-897.5	20	1843.1	1.1	0.36	
Fruit	Huckleberry	Null	-414.753	9	849.1	6.5	0.02
		Baseline null	-410.15	11	844.7	2.1	0.19
		Forest type	-407.888	12	842.6	0.0	0.52
		Forest type with retention	-407.31	13	843.9	1.3	0.27

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**Table A3** (continued)

Type	Species	Model name	LL	k	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	w <sub>i</sub>
	Blueberry	Null	-876.054	13	1781.4	20.6	0.00
		Baseline null	-864.605	18	1771.7	10.9	0.00
		Forest type	-856.326	20	1760.8	0.0	0.74
		Forest type with retention	-855.944	21	1762.9	2.1	0.25
	Lingonberry	Null	-816.223	11	1656.8	4.3	0.06
		Baseline null	-810.337	14	1652.5	0.0	0.49
		Forest type	-808.844	16	1654.8	2.2	0.16
		Forest type with retention	-806.873	17	1653.5	1.0	0.30
	Raspberry	Null	-426.1	10	874.1	7.4	0.02
		Baseline null	-422.206	12	871.2	4.5	0.08
		Forest type	-417.457	14	866.8	0.0	0.71
		Forest type with retention	-417.431	15	869.3	2.5	0.20

**Table A4**

Model log-likelihood (LL), number of estimated parameters (k), small sample size corrected Akaike’s Information Criterion (AIC<sub>c</sub>), AIC<sub>c</sub> difference (ΔAIC<sub>c</sub>), and Akaike weight (w<sub>i</sub>) from stage two logistic regression models that explained variation in the occurrence of grizzly bear foods.

Type	Species	Model name	LL	k	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	w <sub>i</sub>
Forb	Horsetail	Baseline null	-766.1	10	1554.1	3.4	0.13
		Cutblock edge distance	-765.3	11	1554.9	4.2	0.09
		Cutblock or retention edge distance	-765.9	11	1556.2	5.6	0.05
		Cutblock edge distance interaction	-762.5	15	1559.5	8.8	0.01
		Cutblock or retention edge distance interaction	-758.1	15	1550.7	0.0	0.73
	Cow parsnip	Baseline null	-413.8	8	844.9	11.1	0.00
		Cutblock edge distance	-408.9	9	837.3	3.6	0.14
		Cutblock or retention edge distance	-407.1	9	833.7	0.0	0.85
		Cutblock edge distance interaction	-	-	-	-	-
		Cutblock or retention edge distance interaction	-	-	-	-	-
Shrub	Huckleberry	Baseline null	-595.9	9	1211.5	5.9	0.03
		Cutblock edge distance	-593.1	10	1208.2	2.6	0.14
		Cutblock or retention edge distance	-592.9	10	1207.7	2.1	0.18
		Cutblock edge distance interaction	-588.1	13	1205.6	0.0	0.51
		Cutblock or retention edge distance interaction	-589.4	13	1208.1	2.5	0.14
	Blueberry	Baseline null	-481.3	10	984.5	8.6	0.01
		Cutblock edge distance	-479.1	11	982.6	6.6	0.03
		Cutblock or retention edge distance	-479.1	11	982.6	6.6	0.03
		Cutblock edge distance interaction	-477.2	14	986.3	10.4	0.01
		Cutblock or retention edge distance interaction	-472.0	14	975.9	0.0	0.92
	Lingonberry	Baseline null	-655.9	13	1341.2	10.9	0.00
		Cutblock edge distance	-650.4	14	1332.6	2.3	0.23
		Cutblock or retention edge distance	-649.2	14	1330.3	0.0	0.74
		Cutblock edge distance interaction	-648.5	18	1339.5	9.2	0.01
		Cutblock or retention edge distance interaction	-647.9	18	1338.2	8.0	0.01
	Raspberry	Baseline null	-392.4	11	809.2	0.0	0.30
		Cutblock edge distance	-391.3	12	809.4	0.2	0.27
		Cutblock or retention edge distance	-391.6	12	809.9	0.7	0.21
		Cutblock edge distance interaction	-388.7	15	811.8	2.5	0.09
		Cutblock or retention edge distance interaction	-388.3	15	811.0	1.8	0.13
Fruit	Huckleberry	Baseline null	-222.7	7	460.5	5.2	0.04
		Cutblock edge distance	-219.0	8	455.2	0.0	0.52
		Cutblock or retention edge distance	-219.4	8	456.0	0.8	0.35
		Cutblock edge distance interaction	-219.2	10	460.3	5.1	0.04
		Cutblock or retention edge distance interaction	-219.0	10	460.0	4.8	0.05
	Blueberry	Baseline null	-310.6	9	640.8	9.5	0.01
		Cutblock edge distance	-304.7	10	631.3	0.0	0.66
		Cutblock or retention edge distance	-305.8	10	633.5	2.2	0.22
		Cutblock edge distance interaction	-302.9	13	635.1	3.9	0.10
		Cutblock or retention edge distance interaction	-304.7	13	638.6	7.3	0.02
	Lingonberry	Baseline null	-355.4	8	728.0	14.8	0.00
		Cutblock edge distance	-347.9	9	715.4	2.2	0.23
		Cutblock or retention edge distance	-346.8	9	713.2	0.0	0.68
		Cutblock edge distance interaction	-347.9	11	720.1	6.8	0.02
		Cutblock or retention edge distance interaction	-346.8	11	717.9	4.6	0.07
	Raspberry	Baseline null	-187.8	8	392.8	0.0	0.31
		Cutblock edge distance	-187.3	9	394.2	1.4	0.15
		Cutblock or retention edge distance	-186.6	9	392.9	0.1	0.30
		Cutblock edge distance interaction	-185.0	11	394.3	1.5	0.15
		Cutblock or retention edge distance interaction	-185.3	11	395.0	2.2	0.10

**Table A5**

Model log-likelihood (LL), number of estimated parameters (*k*), small sample size corrected Akaike’s Information Criterion (AIC<sub>c</sub>), AIC<sub>c</sub> difference (ΔAIC<sub>c</sub>), and Akaike weight (*w*<sub>i</sub>) from stage two zero-inflated negative binomial models that explained variation in the abundance of grizzly bear foods.

Type	Species	Model name	LL	<i>k</i>	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	<i>w</i> <sub>i</sub>	
Forb	Horsetail	Baseline null	-2519.3	22	5092.7	0.0	0.66	
		Cutblock edge distance	-2519.3	23	5095.6	2.9	0.15	
		Cutblock or retention edge distance	-2519.2	23	5095.4	2.7	0.17	
		Cutblock edge distance interaction	-2517.5	26	5101.6	8.9	0.01	
		Cutblock or retention edge distance interaction	-2517.9	26	5102.2	9.5	0.01	
	Cow parsnip	Baseline null	-871.2	17	1782.1	21.4	0.00	
		Cutblock edge distance	-870.8	19	1786.8	26.1	0.00	
		Cutblock or retention edge distance	-871.1	19	1787.6	26.9	0.00	
		Cutblock edge distance interaction	-851.8	23	1760.7	0.0	0.90	
		Cutblock or retention edge distance interaction	-854.1	23	1765.2	4.5	0.10	
Shrub	Huckleberry	Baseline null	-1380.2	19	2805.7	0.0	0.45	
		Cutblock edge distance	-1380.2	20	2808.5	2.8	0.11	
		Cutblock or retention edge distance	-1379.1	20	2806.4	0.7	0.31	
		Cutblock edge distance interaction	-1380.0	21	2811.2	5.5	0.03	
		Cutblock or retention edge distance interaction	-1378.8	21	2808.6	2.9	0.10	
	Blueberry	Baseline null	-1294.4	22	2642.8	0.0	0.46	
		Cutblock edge distance	-1293.3	23	2643.6	0.8	0.32	
		Cutblock or retention edge distance	-1294.1	23	2645.2	2.4	0.14	
		Cutblock edge distance interaction	-1291.8	25	2646.9	4.1	0.06	
		Cutblock or retention edge distance interaction	-1293.0	25	2649.2	6.4	0.02	
	Lingonberry	Baseline null	-1716.5	19	3478.4	4.5	0.06	
		Cutblock edge distance	-1713.7	20	3475.6	1.7	0.25	
		Cutblock or retention edge distance	-1712.9	20	3473.9	0.0	0.60	
		Cutblock edge distance interaction	-1712.6	22	3479.2	5.3	0.04	
		Cutblock or retention edge distance interaction	-1712.4	22	3478.9	5.0	0.05	
	Raspberry	Baseline null	-898.3	19	1841.9	6.0	0.02	
		Cutblock edge distance	-894.5	20	1837.2	1.3	0.23	
		Cutblock or retention edge distance	-894.3	20	1836.7	0.8	0.29	
		Cutblock edge distance interaction	-891.0	22	1835.9	0.0	0.44	
		Cutblock or retention edge distance interaction	-893.9	22	1841.7	5.8	0.02	
	Fruit	Huckleberry	Baseline null	-407.9	12	842.6	0.9	0.24
			Cutblock edge distance	-406.2	13	841.7	0.0	0.38
			Cutblock or retention edge distance	-406.7	13	842.8	1.1	0.21
			Cutblock edge distance interaction	-406.2	14	844.2	2.5	0.11
Cutblock or retention edge distance interaction			-406.6	14	845.1	3.5	0.07	
Blueberry		Baseline null	-857.9	19	1761.0	0.0	0.58	
		Cutblock edge distance	-857.5	20	1763.1	2.1	0.20	
		Cutblock or retention edge distance	-857.9	20	1763.9	2.8	0.14	
		Cutblock edge distance interaction	-856.9	22	1767.9	6.9	0.02	
		Cutblock or retention edge distance interaction	-855.7	22	1765.5	4.5	0.06	
Lingonberry		Baseline null	-810.3	14	1652.5	0.0	0.54	
		Cutblock edge distance	-810.0	15	1654.5	1.9	0.20	
		Cutblock or retention edge distance	-809.8	15	1654.0	1.4	0.26	
		Cutblock edge distance interaction	–	–	–	–	–	
		Cutblock or retention edge distance interaction	–	–	–	–	–	
Raspberry		Baseline null	-417.5	14	866.8	5.9	0.03	
		Cutblock edge distance	-414.4	15	863.2	2.4	0.19	
		Cutblock or retention edge distance	-413.2	15	860.9	0.0	0.61	
		Cutblock edge distance interaction	-414.3	17	868.4	7.5	0.01	
		Cutblock or retention edge distance interaction	-411.9	17	863.5	2.6	0.16	

**Table A6**

Estimates (beta and standard error) of the best fitting logistic regression models from stage two analysis that explained variation in the occurrence of forb species in relation to competing vegetation, environmental conditions, forest type, and habitat edge distance.

Factor	Variable	Horsetail		Cow parsnip	
		β	SE	β	SE
Competing vegetation	Forb	0.014	0.006		
	GrSd	0.019	0.007		
	ShrS			-0.014	0.008
	ShrT			0.023	0.006
Environmental conditions	Asp10	-3.95E-04	1.16E-03	2.16E-03	1.38E-03
	Asp10 <sup>2</sup>	3.48E-05	1.43E-05	5.95E-05	1.68E-05
	Slp10			0.414	0.113
	Slp10 <sup>2</sup>			-0.015	0.007
	Wam	-0.057	0.012	-0.044	0.018
Forest type	CutY <sub>11-20</sub>	0.925	0.425		
	CutO	0.452	0.546		
	Uncut	0.126	0.423		

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**Table A6** (continued)

Factor	Variable	Horsetail		Cow parsnip	
		$\beta$	SE	$\beta$	SE
Edge distance Interactions	Ret	0.967	0.344		
	RetEdDist	0.025	0.01	0.017	0.006
	CutY <sub>11-20</sub> × RetEdDist	-0.016	0.015		
	CutO × RetEdDist	-0.042	0.015		
	Uncut × RetEdDist	-0.032	0.013		
	Ret × RetEdDist	-0.046	0.016		
	Constant	-0.661	0.358	-3.976	0.665

**Table A7**

Estimates (beta and standard error) of the best fitting logistic regression models from stage two analysis that explained variation in the occurrence of shrub species in relation to competing vegetation, environmental conditions, forest type, and habitat edge distance.

Factor	Variable	Huckleberry		Blueberry		Lingonberry		Raspberry	
		$\beta$	SE	$\beta$	SE	$\beta$	SE	$\beta$	SE
Competing vegetation	Forb			-0.032	0.01	-0.041	0.008		
	GrSd	-0.038	0.009	-0.047	0.015	-0.038	0.009		
	SmlT			-0.02	0.009				
	ShrS	-0.013	0.004	-0.012	0.005	0.051	0.012	-0.035	0.009
	ShrS <sup>2</sup>					-0.001	0		
Environmental conditions	ShrT					-0.027	0.009	0.017	0.007
	Elev	3.88E-03	1.15E-03	-8.43E-03	1.79E-03	3.45E-03	1.37E-03	-5.73E-03	1.53E-03
	Asp1					-1.76E-03	9.43E-04		
	Asp10							9.04E-04	1.20E-03
	Asp10 <sup>2</sup>							4.06E-05	1.24E-05
	Slp1	0.24	0.06						
	Slp1 <sup>2</sup>	-9.09E-03	2.41E-03						
	Slp10							0.34	0.108
	Slp10 <sup>2</sup>							-0.014	0.006
	Wam			-0.034	0.019	-0.069	0.015		
Forest type	CutY <sub>11-20</sub>					0.903	0.428		
	CutO	-0.022	0.459	-1.071	0.568	0.373	0.422	-1.765	0.362
	Uncut	-0.711	0.362	-0.657	0.429	1.013	0.331	-2.417	0.431
	Ret	-1.255	0.348	-0.646	0.53	0.189	0.343	-1.451	0.375
Edge distance	CbEdDist10	0.18	0.24						
	RetEdDist			-0.013	0.009	-0.015	0.005		
Interactions	CutO × RetEdDist			0.027	0.017				
	Uncut × RetEdDist			0.009	0.011				
	Ret × RetEdDist			-0.231	0.07				
	CutO × CbEdDist10	-1.205	0.576						
	Uncut × CbEdDist10	0.536	0.399						
	Ret × CbEdDist10	0.296	0.429						
	Constant	-6.214	1.394	10.017	2.091	-3.981	1.589	4.923	1.666

**Table A8**

Estimates (beta and standard error) of the best fitting logistic regression models from stage two analysis that explained variation in the occurrence of fruit species in relation to competing vegetation, environmental conditions, forest type, and habitat edge distance.

Factor	Variable	Huckleberry		Blueberry		Lingonberry		Raspberry	
		$\beta$	SE	$\beta$	SE	$\beta$	SE	$\beta$	SE
Competing vegetation	Forb			-0.058	0.011	-0.038	0.011		
	GrSd	-0.055	0.023	-0.055	0.024	-0.102	0.034		
	ShrS			-0.013	0.006			-0.032	0.013
	ShrT					-0.037	0.023		
Environmental conditions	Elev	3.724E-03	1.849E-03	-8.658E-03	1.876E-03	3.117E-03	1.302E-03	-7.766E-03	1.915E-03
	Slp10	0.682	0.234					0.200	0.147
	Slp10 <sup>2</sup>	-0.038	0.013					-0.013	0.008
	Wam			-0.036	0.027	-0.076	0.017	0.071	0.011
Forest type	CutY <sub>11-20</sub>			-0.693	0.535				
	CutO	-1.747	1.018	-1.867	0.655	-1.902	1.072	-2.130	0.755
	Uncut	-0.064	0.463	-1.754	0.486	-0.111	0.312	-2.234	0.444
Edge distance	CbEdDist			-0.019	0.008				
	CbEdDist10	0.750	0.363						
	RetEdDist					-0.025	0.008		
	Constant	-9.761	2.014	10.437	2.338	-3.751	1.478	6.288	2.110

**Table A9**

Estimates (beta and standard error) of the best fitting zero-inflated negative binomial regression models from stage two analysis that explained variation in the abundance of forb species in relation to competing vegetation, environmental conditions, forest type, and habitat edge distance.

Factor	Variable	Horsetail		Cow parsnip	
		$\beta$	SE	$\beta$	SE
Competing vegetation	SmlT	-0.006	0.006	-0.036	0.009
	ShrT			0.008	0.004
Environmental conditions	Asp10			0.002	0.001
	Wam	-0.036	0.011		
Forest age or type	CutY <sub>11-20</sub>			1.905	0.352
	CutO	-0.518	0.235	1.391	0.413
	Uncut	-0.191	0.237	1.242	0.31
	Ret	0.635	0.175	1.135	0.45
Edge distance Interactions	CbEdDist10			1.441	0.356
	CutY <sub>11-20</sub> × CbEdDist10			-3.737	0.563
	CutO × CbEdDist10			-2	0.451
	Uncut × CbEdDist10			-2.689	0.542
	Ret × CbEdDist10			-1.21	0.395
	Constant	2.051	0.129	0.025	0.236

**Table A10**

Estimates (beta and standard error) of the best fitting zero-inflated negative binomial regression models from stage two analysis that explained variation in the abundance of shrub species in relation to competing vegetation, environmental conditions, forest type, and habitat edge distance.

Factor	Variable	Huckleberry		Blueberry		Ligonberry		Raspberry	
		$\beta$	SE	$\beta$	SE	$\beta$	SE	$\beta$	SE
Competing vegetation	Forb			-0.038	0.009				
	GrSd			-0.026	0.006				
	SmlT							-0.061	0.013
	ShrS			-0.01	0.004			-0.019	0.008
Environmental conditions	ShrT	-0.011	0.005			-0.017	0.007		
	Elev							-0.005	0.002
	Asp1			0.001	0.001				
	Slp10	0.35	0.101						
Forest type	Slp10 <sup>2</sup>	-0.019	0.007						
	Wam							0.055	0.01
	CutO					-0.67	0.291	-1.206	0.442
	CutYO			-0.447	0.182				
Edge distance	Uncut	0.505	0.2	-0.542	0.217	0.269	0.194	-0.721	0.508
	CbEdDist10							-0.205	0.301
	RetEdDist					-0.009	0.003		
Interactions	CutO × CbEdDist10							-0.859	0.425
	Uncut × CbEdDist10							-1.176	0.47
	Constant	0.211	0.388	3.629	0.143	1.448	0.17	7.394	1.833

**Table A11**

Estimates (beta and standard error) of the best fitting zero-inflated negative binomial regression models from stage two analysis that explained variation in the abundance of fruit species in relation to competing vegetation, environmental conditions, forest type, and habitat edge distance

Factor	Variable	Huckleberry		Blueberry		Ligonberry		Raspberry	
		$\beta$	SE	$\beta$	SE	$\beta$	SE	$\beta$	SE
Competing vegetation	Forb			-0.037	0.019				
	GrSd			-0.024	0.005				
	ShrS			-0.016	0.008			-0.026	0.006
	ShrT			-0.013	0.003	-0.024	0.012		
Environmental conditions	Elev	0.005	0.015			0.004	0.018		
	Slp1			-0.019	0.018				
	Slp10							-0.055	0.026
	Wam	-0.036	0.002			-0.05	0.002		
Forest type	CutYO			-0.914	0.31			-0.391	0.267
	Uncut	0.909	0.429	-0.917	0.31			-1.036	0.286
Edge distance	RetEdDist10							0.661	0.269
	Constant	-4.715	2.507	5.091	0.313	-2.051	1.899	3.062	0.245

**Table A12**

Estimates (mean and standard deviation) of root mean square error (RMSE), mean absolute error (MAE), and pseudo  $R^2$  (Efron's) derived from 10-fold cross validation of the best fitting stage one AIC<sub>c</sub> selected logistic regression and zero-inflated negative models that explained variation in the occurrence and abundance of grizzly bear foods.

Model	Group	Species	RMSE		MAE		R <sup>2</sup>	
			$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Logit	Forb	Horsetail	0.47	0.01	0.43	0.01	0.13	0.05
		Cow parsnip	0.36	0.03	0.26	0.02	0.15	0.09
	Shrub	Huckleberry	0.40	0.02	0.32	0.02	0.10	0.05
		Blueberry	0.35	0.02	0.25	0.02	0.17	0.07
		Ligonberry	0.42	0.02	0.36	0.02	0.21	0.06
	Fruit	Raspberry	0.36	0.03	0.26	0.02	0.25	0.08
		Huckleberry	0.22	0.03	0.09	0.02	0.04	0.04
		Blueberry	0.27	0.03	0.15	0.02	0.14	0.08
		Ligonberry	0.29	0.03	0.17	0.02	0.09	0.05
		Raspberry	0.23	0.04	0.11	0.02	0.15	0.10
ZINB	Forb	Horsetail	7.99	1.97	4.48	0.52	0.10	0.07
		Cow parsnip	2.87	0.64	1.38	0.22	0.23	0.16
	Shrub	Huckleberry	4.66	1.12	2.35	0.37	0.05	0.03
		Blueberry	8.42	1.42	4.14	0.65	0.14	0.09
		Ligonberry	3.64	0.75	2.06	0.23	0.15	0.07
	Fruit	Raspberry	4.00	1.73	1.53	0.37	0.27	0.15
		Huckleberry	2.54	0.98	0.76	0.18	0.04	0.05
		Blueberry	20.83	6.82	7.27	1.42	0.23	0.15
		Ligonberry	5.84	1.59	2.40	0.45	0.08	0.06
		Raspberry	4.20	1.22	1.48	0.38	0.17	0.17

**Table A13**

Estimates (mean and standard deviation) of root mean square error (RMSE), mean absolute error (MAE), and pseudo  $R^2$  (Efron's) derived from 10-fold cross validation of the best fitting stage two AIC<sub>c</sub> selected logistic regression and zero-inflated negative models that explained variation in the occurrence and abundance of grizzly bear foods.

Model	Group	Species	RMSE		MAE		R <sup>2</sup>	
			$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Logit	Forb	Horsetail	0.47	0.01	0.43	0.02	0.14	0.06
		Cow parsnip	0.36	0.03	0.26	0.02	0.16	0.07
	Shrub	Huckleberry	0.40	0.02	0.31	0.02	0.11	0.05
		Blueberry	0.35	0.02	0.25	0.02	0.17	0.06
		Ligonberry	0.42	0.04	0.35	0.04	0.21	0.06
	Fruit	Raspberry	0.36	0.04	0.26	0.04	0.25	0.09
		Huckleberry	0.21	0.04	0.09	0.01	0.05	0.05
		Blueberry	0.27	0.03	0.14	0.02	0.17	0.09
		Ligonberry	0.29	0.04	0.17	0.02	0.12	0.05
		Raspberry	0.23	0.05	0.11	0.02	0.15	0.10
ZINB	Forb	Horsetail	7.99	1.93	4.48	0.57	0.11	0.07
		Cow parsnip	2.75	0.68	1.32	0.26	0.27	0.17
	Shrub	Huckleberry	4.64	1.24	2.35	0.33	0.05	0.04
		Blueberry	8.38	1.65	4.15	0.66	0.15	0.09
		Ligonberry	3.57	0.87	2.03	0.30	0.15	0.06
	Fruit	Raspberry	3.97	1.77	1.55	0.37	0.24	0.15
		Huckleberry	2.50	1.08	0.76	0.20	0.05	0.05
		Blueberry	20.78	7.09	7.30	1.58	0.22	0.16
		Ligonberry	5.79	1.67	2.38	0.45	0.07	0.05
		Raspberry	4.02	1.41	1.39	0.38	0.22	0.19

**Table A14**

Estimates (mean and standard deviation) from 10-fold cross validation for the percentage of correctly classified, rates of false positive and negative, deviations from known occurrence, and area under the receiver operating curve (AUC) derived from the best fitting stage one AICc selected logistic regression models that explained the occurrence of grizzly bear foods. Classification statistics were calculated using cutoff probabilities where sensitivity ‘crossed’ specificity.

Group	Species	Cutoff	Correctly classified		False positive rate <sup>1</sup>		False negative rate <sup>2</sup>		Deviations from known occurrence		AUC	
			$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Forb	Horsetail	0.48	63.36	0.18	39.51	0.34	33.98	0.34	+1.28	0.29	0.70	0.05
	Cow parsnip	0.19	67.52	0.53	134.08	2.28	8.25	0.30	+19.15	0.47	0.74	0.06
Shrub	Huckleberry	0.24	65.24	0.44	116.87	1.41	10.70	0.33	+18.21	0.37	0.71	0.05
	Blueberry	0.22	70.50	0.78	540.00	16.82	1.72	0.21	+15.39	0.31	0.79	0.06
	Ligonberry	0.37	74.61	0.16	112.36	0.91	6.11	0.23	+8.77	0.35	0.77	0.04
Fruit	Raspberry	0.25	74.23	0.27	246.15	2.61	2.80	0.10	+13.41	0.35	0.82	0.05
	Huckleberry	0.06	71.56	0.24	54.41	0.58	14.94	0.34	+26.24	0.99	0.76	0.08
	Blueberry	0.10	71.94	0.30	235.80	2.84	3.53	0.11	+20.69	0.25	0.81	0.06
	Ligonberry	0.14	75.65	0.40	85.53	1.54	7.02	0.21	+21.76	0.33	0.77	0.06
	Raspberry	0.09	78.56	0.45	297.73	5.86	1.75	0.10	+18.18	0.35	0.83	0.09

<sup>1</sup> Rate of false positive is the number of subplots where a species was incorrectly classified as being present by the model divided by the known number of species occurrences.

<sup>2</sup> Rate of false negative is the number of subplots where a species was incorrectly classified as being absent by the model divided by the known number of species absences.

**Table A15**

Estimates (mean and standard deviation) from 10-fold cross validation for the percentage of correctly classified, rates of false positive and negative, deviations from known occurrence, and area under the receiver operating curve (AUC) derived from the best fitting stage two AICc selected logistic regression models that explained the occurrence of grizzly bear foods. Classification statistics were calculated using cutoff probabilities where sensitivity ‘crossed’ specificity.

Group	Species	Cutoff	Correctly classified		False positive rate <sup>1</sup>		False negative rate <sup>2</sup>		Deviations from known occurrence		AUC	
			$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Forb	Horsetail	0.49	64.14	0.32	38.15	0.21	33.75	0.49	+0.75	0.22	0.70	0.04
	Cow parsnip	0.18	68.90	0.23	129.69	1.35	7.59	0.14	+18.84	0.33	0.76	0.06
Shrub	Huckleberry	0.23	64.41	0.36	121.21	1.20	10.50	0.19	+19.35	0.25	0.71	0.05
	Blueberry	0.22	73.35	0.37	117.78	1.80	6.45	0.23	+16.09	0.39	0.80	0.05
	Ligonberry	0.37	71.38	0.29	55.02	0.61	14.90	0.21	+9.01	0.20	0.77	0.04
Fruit	Raspberry	0.25	75.31	0.44	85.89	1.63	7.35	0.28	+13.24	0.40	0.82	0.05
	Huckleberry	0.06	69.60	0.42	554.69	7.80	1.86	0.09	+26.86	0.40	0.77	0.09
	Blueberry	0.11	74.78	0.30	239.83	3.28	2.86	0.09	+20.04	0.33	0.82	0.07
	Ligonberry	0.13	73.61	0.30	221.45	3.08	3.35	0.14	+20.40	0.39	0.79	0.06
	Raspberry	0.09	78.29	0.27	301.52	5.15	1.77	0.16	+18.41	0.46	0.83	0.08

<sup>1</sup> Rate of false positive is the number of subplots where a species was incorrectly classified as being present by the model divided by the known number of species occurrences.

<sup>2</sup> Rate of false negative is the number of subplots where a species was incorrectly classified as being absent by the model divided by the known number of species absences.

**Table A16**

Pearson’s correlation (r) and Spearman’s rank correlation (p) coefficient and calibration (b is the intercept and m is the gradient of the fitted line from linear regression) statistics calculated from the best fitting stage one AICc selected zero-inflated negative binomial models that explained the abundance of grizzly bear foods.

Group	Species	Correlation		Calibration	
		r	p	b	m
Forb	Horsetail	0.32	0.37	-0.09	1.02
	Cow parsnip	0.47	0.36	0.02	1.05
Shrub	Huckleberry	0.21	0.33	0.43	0.73
	Blueberry	0.38	0.40	0.18	0.92
	Ligonberry	0.37	0.48	-0.16	1.10
Fruit	Raspberry	0.49	0.51	-0.16	1.26
	Huckleberry	0.22	0.23	0.13	0.92
	Blueberry	0.47	0.33	-0.73	1.18
	Ligonberry	0.26	0.33	0.23	0.84
	Raspberry	0.41	0.33	-0.01	1.11

**Table A17**

Pearson's correlation (r) and Spearman's rank correlation (p) coefficient and calibration (b is the intercept and m is the gradient of the fitted line from linear regression) statistics calculated from the best fitting stage two AIC<sub>c</sub> selected zero-inflated negative binomial models that explained the abundance of grizzly bear foods.

Group	Species	Correlation		Calibration	
		r	p	b	m
Forb	Horsetail	0.32	0.37	-0.09	1.02
	Cow parsnip	0.56	0.39	-0.07	1.15
Shrub	Huckleberry	0.21	0.33	0.43	0.73
	Blueberry	0.38	0.40	0.18	0.92
	Lingonberry	0.38	0.48	-0.16	1.10
Fruit	Raspberry	0.49	0.50	0.02	1.05
	Huckleberry	0.22	0.23	0.13	0.92
	Blueberry	0.47	0.33	-0.74	1.18
	Lingonberry	0.26	0.33	0.23	0.84
	Raspberry	0.47	0.33	-0.07	1.25

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2018.11.031>.

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