



Harvested forests as a surrogate to wildfires in relation to grizzly bear food-supply in west-central Alberta

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ARTICLE INFO

Keywords:

Ursus arctos
Fire
Harvest
Forest
Food
Productivity
Digestible energy
Disturbance

ABSTRACT

Grizzly bear (*Ursus arctos*) populations residing in interior ecosystems of North America are known to frequent harvested areas and areas burnt by wildfires, as both disturbances encourage growth of early seral vegetation preferred by them. This is especially evident in places where there is a paucity of large natural openings and areas with a long history of wildfire suppression, such as the foothill forests of west-central Alberta. Little has been done, however, to directly quantify and compare grizzly bear food-supply in both disturbance types and at early stages of forest regeneration. In this paper, we explore whether harvested areas can act as surrogates to wildfires for grizzly bear food-supply in west-central Alberta, Canada. We sampled known fruit-bearing and herbaceous grizzly bear foods for their occurrence, productivity, and digestible energy supply among post-harvest, post-fire, and mature forests disturbance types, and across very young (~5 yrs), young (~20 yrs), and mid (~60 yrs) age-classes for post-harvest and post-fire disturbances. A variety of foods occurred at greater frequency in post-harvest stands, with the occurrence of most foods explained by the main effects of disturbance and age-class, or in combination with one environmental covariate. Overall, fruit productivity and digestible energy from fruits were highest in the young age-class, whereas forb productivity and digestible energy from forbs were highest in the very young age-class. There were no significant differences in total available digestible energy (fruit + forb) between post-harvest and post-fire stands within any age-class, but significant differences were evident between age-classes. These results suggest that harvested areas can potentially act as a surrogate to wildfires in relation to grizzly bear food-supply, but human access remains a key challenge for harvests given their association with roads. We suggest that harvested areas could be used as management tool to maintain or enhance grizzly bear food-supply and thus contribute to population recovery efforts, especially in areas of wildfire suppression.

1. Introduction

The role of disturbances in influencing ecosystems, species compositions, and populations are well recognized by ecologists and conservation biologists (Sousa, 1984; Petraitis et al., 1989). Disturbances are important drivers of ecosystem dynamics as they alter forest structure (Weber and Flannigan, 1997), increase species richness and diversity (Thom and Seidl, 2016), and change the rate of succession (Attiwill, 1994). Wildfires and forestry are common disturbances in boreal and cordilleran ecosystems that alter the availability of suitable habitat for species that are well adapted to disturbance, with the potential to increase overall biodiversity at local scales (Brawn et al., 2002; Turner, 2010; Fedrowitz et al., 2014).

The grizzly bear (*Ursus arctos* L., 1758) is a large omnivorous

carnivore, which forages on a wide variety of plant and animal foods that vary in availability both seasonally and spatially (López-Alfaro et al., 2015; Stenset et al., 2016; Coogan et al., 2018). Diets of grizzly bear populations residing in interior ecosystems of North America typically contain high proportions of roots and ungulates during the pre-green-up period, and high proportions of herbaceous vegetation in the spring and early summer, with late-summer and early-autumn diets dominated by fruit (Mattson et al., 1991; McLellan and Hovey, 1995; Munro et al., 2006; López-Alfaro et al., 2015). Importantly, grizzly bears have been shown to have varied dietary preferences consisting primarily of lipids, carbohydrates, and proteins (Erlenbach et al., 2014), and mix their diet to consume food resources with complementary nutritional properties (Robbins et al., 2007; Coogan et al., 2014; Coogan et al., 2018). Fruit is an especially critical high-carbohydrate

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<https://doi.org/10.1016/j.foreco.2019.117685>

Received 12 July 2019; Received in revised form 10 October 2019; Accepted 11 October 2019

Available online 19 November 2019

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food resource of grizzly bears in many interior ecosystems of North America (McLellan and Hovey, 1995; Munro et al., 2006), because it allows bears to optimize their diet in a way to maximize weight gain (Coogan et al., 2014; Hertel et al., 2018). Accumulating mass (both fat and lean) is critical for over-winter survival, and is particularly important to hibernating females that produce altricial cubs in the den (Hilderbrand et al., 2000; McLellan, 2011; López-Alfaro et al., 2013). In fact, McLellan (2011) showed that grizzly bears residing in interior North America – and in particular females – with no dietary access to salmon consumed high amounts of fruits (~85%) and had higher densities than those populations that relied more heavily on meat of terrestrial species. Likewise, local grizzly bear densities in west-central Alberta were higher in areas with higher bear amounts of both fruit and ungulates, as opposed to either food resource on its own (Nielsen et al., 2017).

Importantly, areas disturbed by wildfire and forest harvest are frequented by foraging grizzly bears. Grizzly bear populations of interior North America are known to select for a variety of open vegetation and early seral habitats (Herrero, 1972; Hamer and Herrero, 1987). The open-canopy habitats of post-harvest and post-fire stands encourage early seral vegetation, which provides seasonally important foods that include abundant fruit-bearing species (Hamer and Herrero, 1987; McLellan and Hovey, 1995; Nielsen et al., 2004c; Munro et al., 2006). For example, grizzly bears likely benefit from foraging in early seral post-fire stands due to increases in graminoids, forbs, roots, ants, and fruiting shrubs that emerge post disturbance (Martin, 1983; Hamer and Herrero, 1987; McLellan and Hovey, 1995). Likewise, these open-canopy habitats sustain higher ungulate densities (Fisher and Wilkinson, 2005), which are a key dietary component of grizzly bears during the hypophagic period (McLellan and Hovey, 1995; Mattson, 1997; Munro et al., 2006; Stenset et al., 2016). This coupled with the fact that grizzly bear body size and condition are positively related to forestry disturbance (Zedrosser et al., 2006; Nielsen et al., 2013; Bourbonnais et al., 2014) and food resource abundance (Waller and Mace, 1997; Nielsen et al., 2004c) suggest early seral forests are important components shaping grizzly bear condition.

Fire regimes in the Canadian Rocky mountain system tend to be dominated by high-intensity stand-replacing fires (Johnson and Fryer, 1987; Johnson and Larsen, 1991). In contrast, the foothills of west-central Alberta have more mixed-severity fire regimes and less frequent stand-replacing fires (Amoroso et al., 2011). Moreover, widespread fire suppression in the area has reduced the frequency of stand-replacing fires (Andison, 1998; Rogeau et al., 2016). Consequently, this has restricted the availability of open-canopy habitats and early seral forests important to foraging grizzly bears. Thus, grizzly bears inhabiting the foothills have relatively limited access to large natural openings and fewer opportunities to forage for foods important to their diet compared to bears inhabiting mountainous areas (e.g. Canadian Rocky Mountain Parks).

Previous research, however, has shown that grizzly bears inhabiting the foothills frequent harvested areas (Nielsen et al., 2004a), as canopy removal encourages regeneration of early seral vegetation preferred by them (Martin, 1983; Nielsen et al., 2004c). Likewise, ungulates occur at higher densities in landscapes associated with post-harvest stands (Fisher and Wilkinson, 2005). Furthermore, grizzly bear body size and local abundance was noted to be highest in locations with the longest history of forest management, as favorable food supply and habitat diversity are at a greater availability to grizzly bears (Nielsen et al., 2013, 2017). In contrast to the foothills, studies in the Rocky Mountains have documented bears avoiding harvested areas in favor of naturally occurring openings and early seral habitats (Zager et al., 1983; Waller, 1992; McLellan and Hovey, 2001; Apps et al., 2004). A potential explanation for this discrepancy is that grizzly bears inhabiting the foothills have limited access to the same kind of open habitats (e.g. burns,

alpine meadows) that characterize more mountainous populations. Therefore, there may be benefits in exploring whether harvested areas in the foothills can act as surrogates to relatively infrequent stand-replacing fires.

The purpose of this study was to investigate whether harvested areas can act as surrogates to natural wildfire disturbances with respect to grizzly bear food-supply (occurrence, abundance, and digestible energy). Specifically, our objectives were two-fold: (1) quantify differences in food occurrence, overall productivity, and digestible energy of known grizzly bear foods between post-harvest and post-fire stands of three different age-classes; and (2) develop models to evaluate which additional variables, other than disturbance type and age-class contribute to the occurrence of local grizzly bear foods. With respect to quantifying differences in digestible energy, we hypothesized that if harvested areas represent surrogates to wildfires: 1) digestible energy from fruits, digestible energy from forbs, and total (fruit + forb) available digestible energy will not vary between post-harvest and post-fire stands; 2) whereas digestible energy from fruits, digestible energy from forbs, and total available digestible energy will vary between age-classes. We explore these questions in the foothills of west-central Alberta, Canada.

2. Methods

2.1. Study area

The study area (Fig. 1) is located in west-central Alberta, Canada (approximate location 53°24'N, 117°33'W) and includes portions of the eastern slopes of the Rocky Mountains and Foothills, with the western and eastern areas characterized by mountainous terrain and foothills, respectively. We chose this area because wildfire and forestry have been the primary disturbance agents since the 1950s (Andison, 1998). Furthermore, we focused our sampling entirely within the upper foothills subregion because concurrently sampling both the upper and lower foothills subregions was not logistically feasible, and the grizzly bear population density is higher in the upper foothills, with estimates of 5–10 bears per 1000 km² (Boulanger et al., 2018). The upper foothills are distinguished from the lower foothills by higher precipitation and a lower average temperature, and the climate is continental with a mean annual temperature of 1.3 °C and a mean annual precipitation of 632 mm (Natural Regions Committee, 2006). Most of the area is public land managed by the province and zoned for multiples uses, with forestry and development from the energy sector (oil and gas, coal mining) being the primary human activity. The foothills are dominated by forests and support a range of habitats with lodgepole pine (*Pinus contorta*) being the most common tree species. Mesic upland sites at higher elevation are composed of mix stands of lodgepole pine, white spruce (*Picea glauca*), and trembling aspen (*Populus tremuloides*), whereas wet lowland sites at lower elevation are composed of black spruce (*Picea mariana*) and tamarack (*Larix laricina*) bogs.

2.2. Wildfire and forestry

Historically, the eastern slopes of the Rocky Mountains and Foothills were characterized as a mixed-fire severity regime, with frequent low-severity fires overlapping infrequent high-severity fires (Amoroso et al., 2011; Davis et al., 2016; Rogeau et al., 2016). This past century, however, has seen an increase in fire suppression and departure from historical fire regimes leading to less stand-replacing fires and consequently a longer fire cycle (Tande, 1979; Andison, 1998; Davis et al., 2016; Rogeau et al., 2016). With the foothills being dominated by productive forests (Andison, 1998), large-scale timber harvesting has become the main disturbance agent replacing natural wildfire in this region.

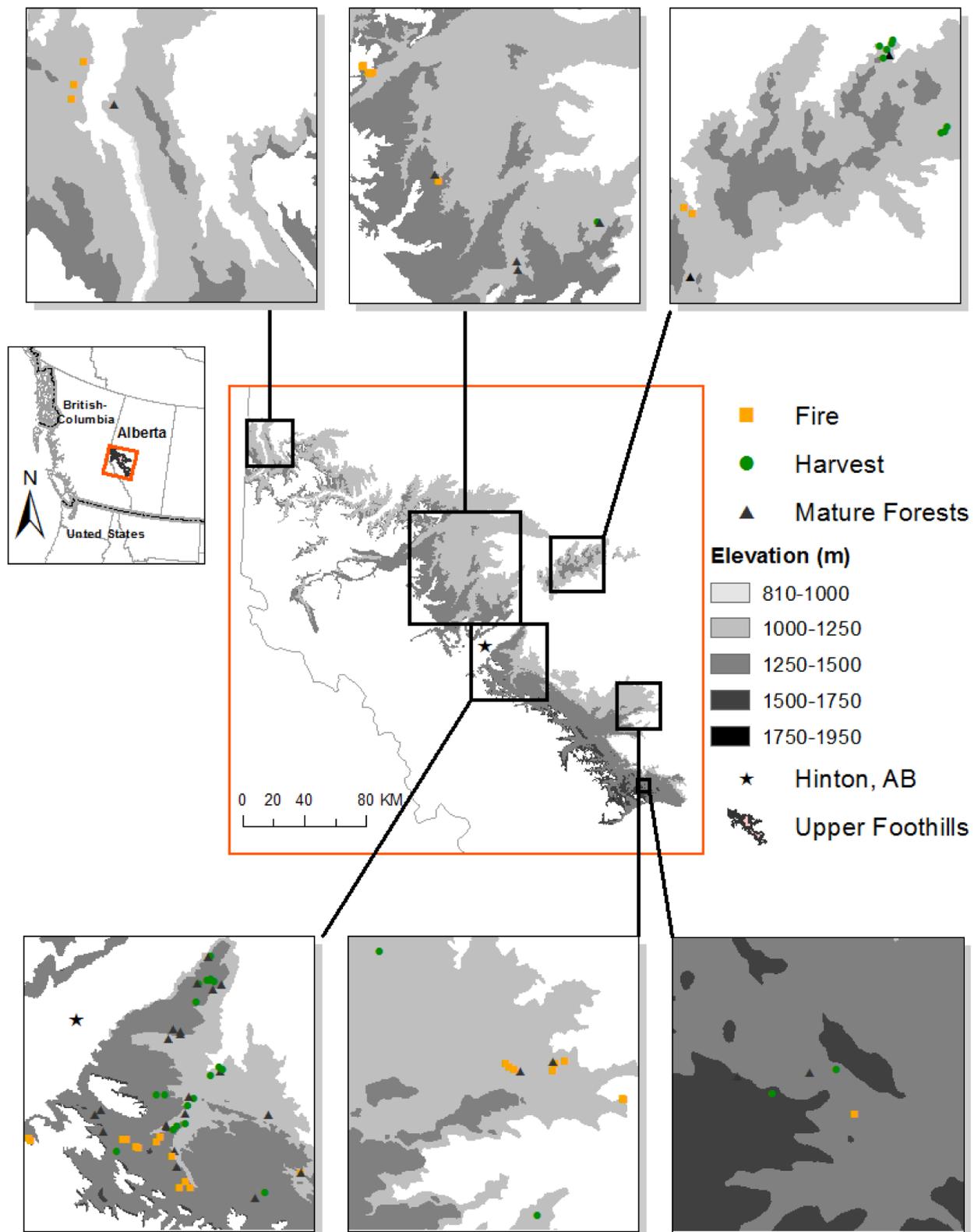


Fig. 1. Study area depicting sampling sites located within the upper foothills subregion of Alberta, Canada. The extent and elevational gradients of the upper foothills are shown, including the location of Hinton, AB. The middle panel shows the full sampling extent and inset boundaries of the upper and lower panels.

2.3. Field plots and data recording

In the summer of 2017 (late June – late August) we sampled 33 sites in each of the three disturbance types: post-harvest stands, post-fire stands, and reference mature forests. All mature forest stands were

largely undisturbed by human activities and dominated by coniferous species, which represents older forests (> 80 years old) in the area (Anderson, 1998). The same sampling procedure was used among the three disturbance types. We used a combination of previously sampled sites (Nielsen et al., 2004c) and a 25-m Landsat-derived wildlife habitat

classification product (approximately 90% of sampled sites; Nijland et al., 2015) to identify random plot coordinates based on forest harvests data (ABMI Human Footprint Inventory, 2016) and wildfire spatial inventory data (Alberta Wildfire, 2017). We randomly stratified plot locations between both post-harvest and post-fire disturbances according to different age-classes, to ensure proportionality of three successional stages (very young: ~5 yrs; young: ~20 yrs; and mid: ~60 yrs). We choose the very young and young age-classes because they are characterized by early seral vegetation, which provides a diverse array of seasonally important foods critical to bear diets (Hamer and Herrero, 1987; McLellan and Hovey, 2001; Nielsen et al., 2004c; Munro et al., 2006), whereas the mid age-class lacks early seral vegetation because of canopy closure related to forest succession (Kneeshaw and Bergeron, 1998). However, we did sample the mid age-class because the occurrence of some species have been shown to increase with canopy cover (e.g. cow parsnip, *Heracleum lanatum*; Nielsen et al., 2004c). Forest age (age-class) was not considered among mature forests because stands are considered to be > 80 years old (Andison, 1998).

At each field-sampling site, we first quantified plant and ant (Formicidae spp.) occurrence within a 50 × 20 m belt transect (0.1 ha) that ran south-to-north. We then estimated the abundance of thirteen berry-producing shrubs and four herbaceous plants (three forbs and one green vegetation) in a 50 × 2 m belt transect (0.01 ha) located within the 0.1 ha belt transect. These bear food items are considered important to the diet of grizzly bears in west-central Alberta (Hamer and Herrero, 1987; Hamer, 1996; Hamer, 1999; McLellan and Hovey, 1995; Nielsen et al., 2004c; Munro et al., 2006). Sweetvetch (*Hedysarum* spp.) roots and ungulate species, as indicated by pellet counts, were recorded, but not further analyzed here because of low prevalence. For ground-dwelling shrubs (< 0.5 m in height) and herbaceous plants, ten herbaceous quadrats (0.5 m²) were established at 5-m intervals along the midline of the belt transect to record percent cover, number of berries, and number of herbaceous plants. Within each quadrat we recorded seven ground-dwelling shrubs and four herbaceous plants. The shrubs include: bearberry (*Arctostaphylos uva-ursi*), strawberry (*Fragaria virginiana*), raspberry (*Rubus idaeus*), dwarf bilberry (*Vaccinium caespitosum*), huckleberry (*Vaccinium membranaceum*), blueberry (*Vaccinium myrtilloides*), and lingonberry (*Vaccinium vitis-idaea*). The herbaceous plants include: horsetail (*Equisetum* spp.), cow parsnip (*Heracleum lanatum*), dandelion (*Taraxacum officinale*), and clover (*Trifolium* spp.). For large shrubs (≥ 0.5 m in height), we not only counted the number of shrubs (density), but also the number of berries that fell within the 2-m belt transect. The shrubs include: black twinberry (*Lonicera involucrata*), currant and gooseberry (*Ribes* spp.), buffaloberry (*Shepherdia canadensis*), western mountain-ash (*Sorbus scopulina*), and lowbursh cranberry (*Viburnum edule*). The recorded presence of ant colonies that occurred in logs, stumps, or mounds were pooled together within the 0.1 ha belt transect. Finally, within each belt transect, canopy cover was measured with a spherical densiometer, as canopy is considered a good predictor of occurrence and abundance of bear food items (Nielsen et al., 2004c). Four measurements from each cardinal direction were taken at 5-m intervals along the midline of the belt transect and averaged within each interval and across the entire transect.

2.4. Statistical analyses

2.4.1. Food occurrence and distribution

We used logistic regression to contrast the occurrence of 18 grizzly bear food items for target (T) and reference (R) categories, that being: post-harvest (T) vs. post-fire (R), post-harvest (T) vs. mature forests (R), and post-fire (T) vs. mature forests (R). Logistic regression results are reported with beta coefficients and odds ratios, with the reference

Table 1

Model structure of eight a priori candidate models used to assess the occurrence of grizzly bear food items in post-harvest and post-fire stands. The covariates include: combined disturbance and age-class (DIST_AGE), elevation (ELEV), canopy cover (CAN), and compound topographic index (CTI).

Model Structure	K
DIST_AGE	2
DIST_AGE + ELEV	3
DIST_AGE + ELEV + CAN	4
DIST_AGE + ELEV + CTI	4
DIST_AGE + CAN	3
DIST_AGE + CTI	3
DIST_AGE + CAN + CTI	4
DIST_AGE + ELEV + CAN + CTI	5

category being post-fire stands when compared to post-harvest stands, and mature forests otherwise. We interpret the odds ratio as the odds that a grizzly bear food item occurred in the target category compared with that of the reference category for each age-class. An odds ratio > 1 can be interpreted as higher occurrence in the target category, whereas an odds ratio < 1 can be interpreted as higher occurrence in the reference category. We grouped species into three broad categories, which include shrub-fruit (plant height ≥ 50 cm), dwarf shrub-fruit (plant height < 50 cm), and forb (including horsetail) and ants.

We also examined the distribution (occurrence) of 18 grizzly bear food items against predictor variables previously used to predict bear food occurrence (Nielsen et al., 2004c; Braid and Nielsen, 2015) in foothills of Alberta. The predictor variables include: combined disturbance and age-class (DIST_AGE), elevation (ELEV), a soil wetness index referred to as the compound topographic index (CTI) that is used as a proxy for soil conditions, and a field-based measure of canopy cover (CAN). We used these predictor variables in combination to develop 8 a priori candidate models (Table 1) and evaluated which model best predicted the occurrence of each food item using Akaike information criteria with a small sample size correction (AICc; Burnham and Anderson, 2002). Collinearity among predictor variables was assessed with Pearson's Correlation (*r*) with all variables assumed to be uncorrelated $r < |0.7|$ (Swets, 1988). We used area under the curve (AUC) of the receiver operating characteristic (ROC) to assess model accuracy (Fawcett, 2006), with AUC values < 0.7 and ≥ 0.7 representing poor model accuracy and good model accuracy, respectively (Swets, 1988).

Finally, we created separate models to estimate and plot the probability of occurrence of each food item in relation to canopy cover using a global model structure with quadratic terms (DIST + AGE + AGE² + CAN + CAN² + ELEV + ELEV² + CTI + CTI²), while holding all other variables in the global model at their mean level. Here, age was treated as continuous variable in order to provide a visual interpretation of the predicted nonlinear responses for both post-harvest and post-fire disturbances.

2.4.2. Food productivity and energy

We assessed fruit (berry) and forb productivity for 17 grizzly bear foods using Mann-Whitney *U*-tests. For each bear food item, we estimated average density on a per hectare basis between post-harvest, post-fire, and mature forests, and among the three age-classes. We did not assess ant density because ant abundance was not recorded in this study.

We estimated the digestible energy from fruit on a per hectare basis

by converting the total number of berries for 12 fruiting species into a measure of digestible energy using the following equations:

$$\text{dig_ene}_i = \text{fruit count} \left(\frac{\text{berry}}{\text{ha}} \right) \times \text{fruit DM}_i \left(\frac{\text{gram DM}}{\text{berry}} \right) \times \text{digestible energy} \left(\frac{\text{kcal}}{\text{gram DM}} \right)$$

$$\text{digestible energy} = \sum_{i=1}^n \text{dig_ene}_i$$

DM = Dry Mass

Digestible energy conversions were obtained from López-Alfaro et al. (2015), and fruit dry weights (mass in g) were estimated using data from the literature (Appendix, Table A1). We also estimated the digestible energy of four herbaceous plants on a per hectare basis by converting percent cover into biomass (g dry weight) using allometric conversion equations (Nielsen et al., 2015), with this further converted into digestible energy following López-Alfaro et al. (2015). We summed digestible energy from fruits and forbs to estimate the total digestible energy available from these foods. Finally, we estimated total available

digestible energy in the upper foothills by multiplying the average energy per hectare by the area disturbed by forestry and fire in the study area, respectively. We did not have access to reliable data needed to estimate average digestible energy per hectare for mature forests.

To evaluate whether digestible energy varied as a function of disturbance and age-class, we conducted three separate two-way ANOVAs that examined the effect of disturbance, age-class, and the interaction between disturbance and age-class (model: $(\text{digestible energy})^{0.5} = \text{disturbance} + \text{age-class} + \text{disturbance} * \text{age-class}$) on digestible energy from fruits, digestible energy from forbs, and total available digestible energy, respectively. All digestible energy variations were square root transformed. We used a *post hoc* Tukey HSD test following a significant ANOVA, where all tests were considered significant at $\alpha \leq 0.05$. We conducted all analyses in R v3.5.0 (R Core Team, 2018).

3. Results

3.1. Food occurrence in harvest and fire

Among the very young age-class, six species had greater presence in

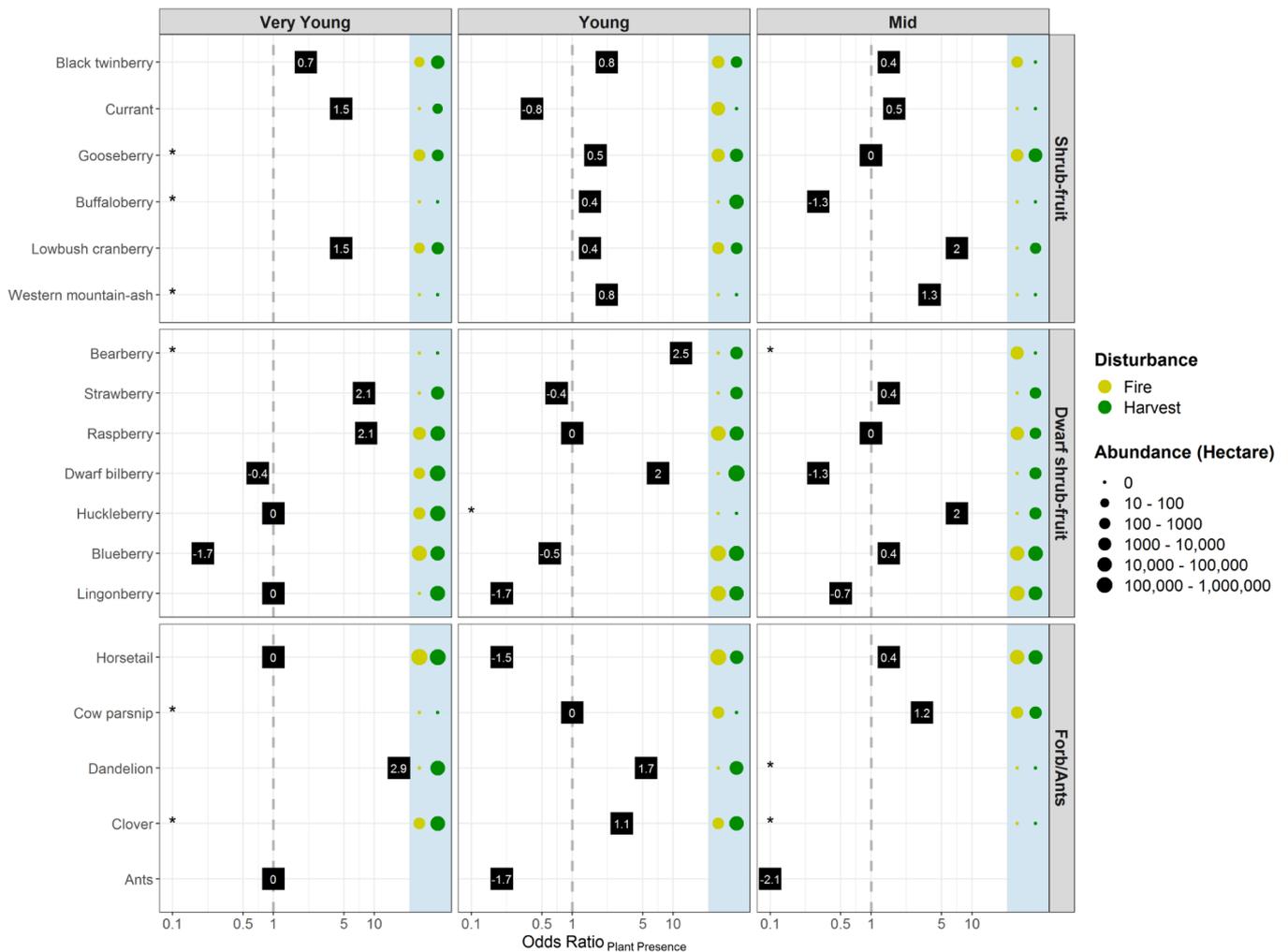


Fig. 2. Estimated odds ratios (black squares) and beta coefficients (white text embedded in black squares) from logistic regression models describing the occurrence of 18 grizzly bear food items between post-harvest and post-fire stands by age-class. Odds ratios represent the odds of finding bear foods items in post-harvest stands compared to post-fire stands within each age-class. Positive beta coefficients indicate a greater occurrence of bear food items in post-harvest stands, whereas negative coefficients indicate greater occurrence in post-fire stands. Colored circles within the shaded section represent the average berry density for shrub-fruit (plant height ≥ 50 cm) and dwarf-shrub fruit (plant height < 50 cm) categories, and the average stem density for the forb and ants category, on a per hectare basis for 17 grizzly bear food items in post-harvest and post-fire stands. Abundance estimates for ants are absent as this was not recorded in this study. Asterisks indicate bear food items with models that failed to converge. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

post-harvest stands compared to post-fire stands (Fig. 2). These species included black twinberry, currant, lowbush cranberry, strawberry, raspberry, and dandelion. Among both the young and mid age-classes, each had nine species with greater presence in post-harvest stands compared to post-fire stands. For the young age-class, these included: black twinberry, gooseberry, buffaloberry, lowbush cranberry, western mountain-ash, bearberry, dwarf bilberry, dandelion, and clover. For the mid age-class, these included: black twinberry, currant, lowbush cranberry, western mountain-ash, strawberry, huckleberry, blueberry, horsetail, and cow parsnip. Overall, only two species had greater presence in post-harvest stands for all three age-classes, which included black twinberry and lowbush cranberry. In general, most species within the shrub-fruit category (plant height ≥ 50 cm) were more likely to occur in post-harvest stands, whereas no clear pattern of presence was evident for species within the dwarf-shrub fruit (plant height < 50 cm) and forb and ants categories, respectively (Fig. 2). As a general pattern, however, and apart from a few exceptions, *Vaccinium* spp. and ants were more likely to occur in post-fire stands compared with post-harvest stands. The average odds ratio for *Vaccinium* spp. (apart from dwarf bilberry in the young age-class and huckleberry the mid age-class) was 0.65 with 95% CIs ranging from a low of 0.1 to a high of 2.6. For ants, the average odds ratio was 0.44 with 95% CIs ranging from a low of 0.1 to a high of 1.8.

3.2. Distribution of foods

Based on AICc rankings in Table 2, there was moderate variation in support of the eight *a priori* candidate models listed in Table 1. Model DIST_AGE ranked highest for five of the eighteen grizzly bear food species, including buffaloberry and huckleberry which are critical bear foods. In contrast, model DIST_AGE + CAN ranked highest for bearberry and ants. Apart from huckleberry, the top ranked models for *Vaccinium* spp. included at least one environmental covariate other than DIST_AGE. Using likelihood ratio (χ^2) tests, we found 12 AICc-selected models (Table 2) to be significant ($\alpha < 0.05$), while six were not found to be significant including: black twinberry, currant, lowbush cranberry, western mountain-ash, raspberry, and horsetail. The percent deviance explained varied from a low of 4.9% for black twinberry to a high of 50.8% for dandelion. Overall, *Vaccinium* spp. and forbs (other than horsetail) generally had higher values of percent deviance explained. Classification accuracy (AUC) proved poor (< 0.7) for 7 of the

18 grizzly bear food species and good (≥ 0.7) for the remaining 11 species.

Overall, nonlinear responses in occurrence against canopy cover (Fig. 4) were similar between post-harvest and post-fire stands for most food items. Buffaloberry peaked at intermediate levels of canopy, while most species categorized as dwarf-shrub fruit (plant height < 50 cm) peaked at lower levels and dropped precipitously at higher levels, except for huckleberry, blueberry, and strawberry. Ants also peaked at lower levels of canopy cover and decreased as canopy increased, while cow parsnip increased with increasing canopy.

3.3. Fruit productivity and digestible energy in harvest and fire

Among all age-classes (Fig. 2), *Vaccinium* spp. and raspberry were often the most productive food items in terms of berry productivity in both post-harvest and post-fire stands, whereas species within the shrub-fruit (plant height ≥ 50 cm) category were not as productive overall. Important grizzly bear foods such as huckleberry and buffaloberry showed contrasting results, with huckleberry being more productive overall. In each age-class, the food items with the highest berry productivity always occurred in post-harvest stands (Fig. 2). Average fruit production peaked in the young age-class for both post-harvest and post-fire stands (Fig. 3; Panel A). When comparing between post-harvest and post-fire stands, berry productivity was highest in the very young and young age-classes of post-harvest stands, whereas the opposite pattern occurred in the mid age-class (Fig. 3; Panel A). Mann-Whitney *U*-tests ($\alpha < 0.05$) revealed that only one species significantly differed in fruit production when comparing between disturbances and among the same age-class. In this case, dwarf bilberry in post-harvest stands of the young age-class differed from post-fire stands of the same age-class ($U = 88, P = 0.016$).

Overall, patterns of digestible energy from fruits were similar to fruit productivity, with digestible energy peaking in the young age-class (Fig. 3; Panel C). When comparing between post-harvest and post-fire stands, digestible energy was highest in very young and young age-classes of post-harvest stands, albeit only marginally for the young age-class. When looking at digestible energy from fruits, the main effect of age-class was significant ($F(2, 60) = 3.693, p = 0.031, \eta_p^2 = 0.110$), whereas the main effect of disturbance was not significant ($F(1, 60) = 1.928, p = 0.170, \eta_p^2 = 0.031$). The interaction effect between disturbance and age-class was likewise not significant ($F(2,60) = 1.598,$

Table 2

AICc top-selected models that best describe the occurrence of 18 grizzly bear food items in post-harvest stands, post-fire stands, and mature forests of west-central Alberta. For each species, an AICc score is provided for both the null and top ranked model, as well as, likelihood ratio (χ^2) tests, statistical significance values (*p*), area under the curve (AUC), and percent deviance explained. List of model structures can be found in Table 1.

Grizzly bear food item		Null model	AICc-selected model					
Category	Species Name	AICc	Model Structure	AICc	LR χ^2	<i>p</i>	AUC	% Dev. Explained
Shrub-fruit	Black twinberry	139.03	DIST_AGE + ELEV	148.15	6.74	0.456	0.66	4.92
	Currant	123.50	DIST_AGE + CTI	126.40	12.66	0.081	0.71	10.42
	Gooseberry	128.07	DIST_AGE	127.29	13.97	0.03	0.69	11.09
	Buffaloberry	101.67	DIST_AGE	98.51	16.35	0.012	0.75	16.41
	Lowbush cranberry	137.57	DIST_AGE + CAN	139.74	13.40	0.063	0.68	9.88
	Western mountain-ash	92.84	DIST_AGE	96.46	9.58	0.144	0.69	10.55
Dwarf shrub-fruit	Bearberry	82.73	DIST_AGE + CAN	68.24	30.05	< 0.001	0.90	37.24
	Strawberry	139.27	DIST_AGE	139.69	12.77	0.047	0.69	9.31
	Raspberry	136.35	DIST_AGE	138.91	10.63	0.1	0.66	7.92
	Dwarf bilberry	128.07	DIST_AGE + CAN + CTI	122.06	23.99	0.002	0.80	19.04
	Huckleberry	113.93	DIST_AGE	108.52	18.6	0.005	0.73	16.62
	Blueberry	126.64	DIST_AGE + ELEV	107.83	34.37	< 0.001	0.84	27.58
	Lingonberry	137.57	DIST_AGE + ELEV + CAN	134.40	21.15	0.007	0.77	15.60
Forb/Ants	Horsetail	135.62	DIST_AGE	139.91	8.89	0.180	0.66	6.66
	Cow parsnip	89.62	DIST_AGE	87.76	15.05	0.020	0.76	17.19
	Dandelion	109.37	DIST_AGE + CTI	70.45	54.48	< 0.001	0.93	50.76
	Clover	111.71	DIST_AGE	81.31	43.58	< 0.001	0.86	39.74
	Ants	125.11	DIST_AGE + CAN	106.32	34.35	< 0.001	0.84	27.91

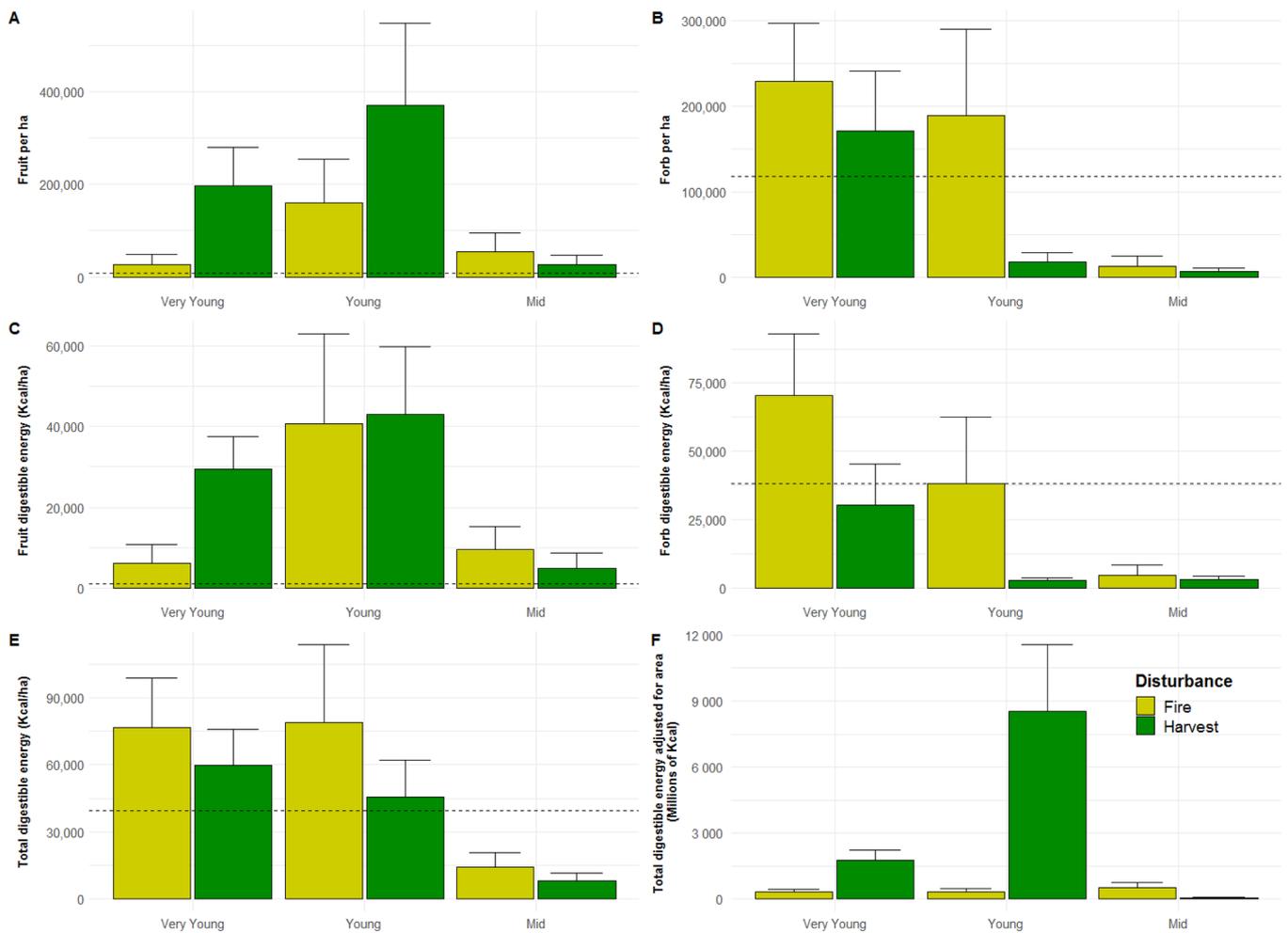


Fig. 3. Productivity and digestible energy differences (+SE) between post-harvest and post-fire stands for each age-class. Panel A depicts fruit (berry) density from 12 fruiting species, excluding western mountain-ash. Panel B depicts forb density from four species (horsetail, cow parsnip, dandelion, and clover). Panel C depicts digestible energy from fruits with the same 12 species used in panel A. Panel D depicts digestible energy from forbs with the same four species used in panel B. Panel E depicts the combined total available digestible energy from fruits and forbs. Panel F depicts total available digestible energy adjusted for actual area of disturbance on the landscape of the upper foothills of our study area. The black dotted lines refer to mature forests; this line is absent from panel F because we did not have access to reliable data needed to estimate this value.

$p = 0.211$, $\eta_p^2 = 0.051$). A *post hoc* Tukey HSD test revealed that the mid age-class significantly differed from the young age-class ($p = 0.023$).

3.4. Forb productivity and digestible energy in harvest and fire

Among the forb and ants category (Fig. 2), horsetail was productive among both disturbances and all age-classes, albeit slightly more productive in post-fire stands. Dandelion and clover were more productive in the very young and young age-classes, whereas cow parsnip was productive in the mid age-class. For both post-harvest and post-fire stands (Fig. 3; Panel B), forb density peaked in the very young age-class. In the young age-class, density dropped precipitously in post-harvest stands and only slightly in post-fire stands. Mann-Whitney *U*-tests ($\alpha < 0.05$) revealed that two species differed in forb productivity between disturbances and among age-classes, including horsetail in the young age-class ($U = 22.5$, $P = 0.001$), and dandelion in the very young age-class ($U = 82.5$, $P = 0.036$).

Overall, patterns of digestible energy from forbs were similar to forb density, with digestible energy peaking in the very young age-class of

both disturbances, and digestible energy levels highest in post-fire stands across all age classes (Fig. 3; Panel D). When looking at digestible energy from forbs, both age-class ($F(2, 60) = 8.966$, $p < 0.001$, $\eta_p^2 = 0.230$) and disturbance ($F(1, 60) = 4.906$, $p = 0.031$, $\eta_p^2 = 0.076$) were significant, whereas the interaction between disturbance and age-class was not significant ($F(2, 60) = 1.426$, $p = 0.248$, $\eta_p^2 = 0.045$). A *post hoc* Tukey HSD test revealed that the very young age-class significantly differed from both the young age-class ($p = 0.028$) and mid age-class ($p < 0.001$), while the young age-class did not significantly differ from the mid age-class ($P = 0.278$).

3.5. Total available digestible energy in harvest and fire

Overall, patterns of total available digestible energy were highest in post-fire stands across all age-classes, with the highest digestible energy levels in the very young and young age-classes for both disturbances (Fig. 3; Panel E). Results indicated that the main effect of age-class was significant ($F(2, 60) = 7.446$, $p = 0.001$, $\eta_p^2 = 0.199$), whereas the main effect of disturbance was not significant ($F(1, 60) = 0.300$, $p = 0.586$, $\eta_p^2 = 0.005$). The interaction between the disturbance and

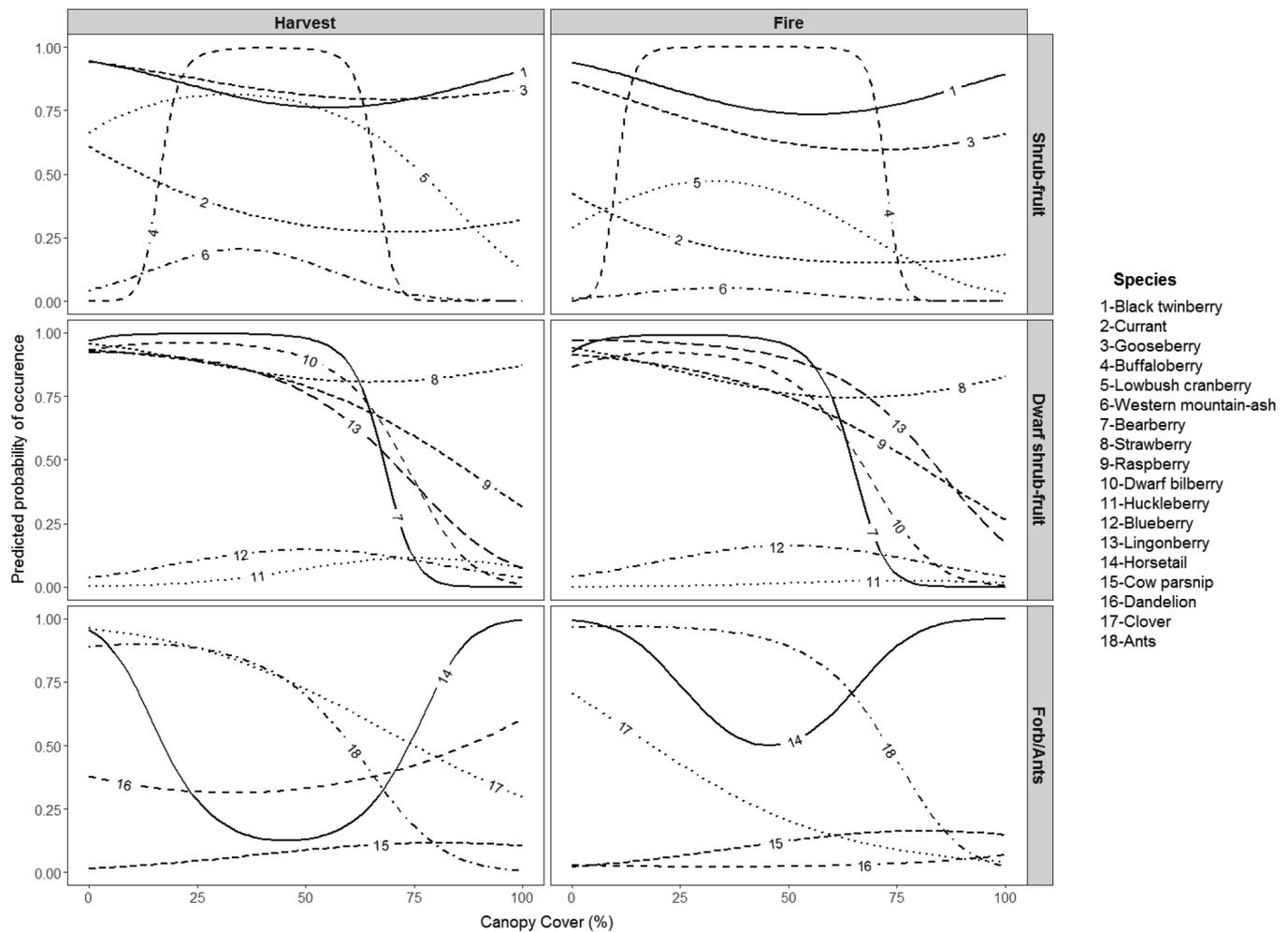


Fig. 4. Predicted probability of occurrence of bear food items as a function of canopy cover in post-harvest and post-fire stands. Environmental covariates in the global model were held at their mean level. Numbers embedded within each line correspond to the associated bear food item located within the legend.

age-class was also not significant ($F(2, 60) = 0.003, p = 0.997, \eta_p^2 = 0$). A post hoc Tukey HSD test revealed that the mid age-class significantly differed from both the very young ($p = 0.021$) and young age-classes ($p = 0.001$). When adjusting total available digestible energy in each disturbance and age-class for actual area disturbed in the upper foothills of our study area, we found that the amount of total available digestible energy was approximately $5\times$ greater in the very young age-class and $26\times$ greater in young age-class of post-harvest stands. In contrast, total available digestible energy was approximately $9\times$ greater in the mid age-class of post-fire stands (Fig. 3; Panel F).

4. Discussion

Our results suggest that harvested areas can potentially act as a surrogate to wildfire disturbances for grizzly bears inhabiting west-central Alberta. Grizzly bears in the study area have been shown to select for harvested areas (Nielsen et al., 2004a) – similar to bears in other parts of interior of North America (Giarniello et al., 2007) and Scandinavia (Moe et al., 2007) – which provide a diverse range of food resources (Martin, 1983; Nielsen et al., 2004c) needed for optimal dietary intake (Robbins et al., 2007; Coogan et al., 2014), with this complementary diet being positively associated with local population density (Nielsen et al., 2017) and fitness (McLellan, 2011; Erlenbach et al., 2014). Because west-central Alberta generally lacks large

naturally occurring open-canopy habitats, harvested areas may be an attractive alternative to bears on a fire-suppressed landscape. Indeed, sites disturbed by humans may allow bears to exploit preferred foods on habitats that are functionally similar to large natural openings and early seral fire-regenerated habitats (Nielsen et al., 2004a). For instance, in Yellowstone National Park, declines in cutthroat trout has paralleled an increase in predation rates on elk neonates (Middleton et al., 2013), suggesting a shift in grizzly bear foraging behavior as a consequence of human actions. Even so, any benefits that bears derive from foraging in harvested areas may be offset by an elevated mortality risk due to increased human access, primarily via roads (Nielsen et al., 2004b; Boulanger and Stenhouse, 2014).

When comparing the occurrence of food items in post-harvest and post-fire stands, only black twinberry and lowbush cranberry occurred at higher frequencies in post-harvest stands for all three age-classes. Harvesting appeared to benefit these large shrub species, suggesting that rhizome disturbance and canopy removal may help explain deviation from post-fire stands. Overall, a greater number of species occurred at higher frequencies in the young and mid age-classes compared to the very young age-class, suggesting canopy cover is positively related to the occurrence of a greater number of species overall (Nielsen et al., 2004c). In contrast, blueberry and lingonberry were more likely to occur in post-fire stands, suggesting that harvesting negatively affected their occurrence, especially among the very young and young

Table 3

Odds ratios describing the occurrence of important grizzly bear food items in post-fire and post-harvest stands compared to mature forests alone, with 95% confidence intervals in parentheses. Asterisks indicate no recorded presence.

Species	Very Young		Young		Mid	
	Fire	Harvest	Fire	Harvest	Fire	Harvest
Buffaloberry	*	*	2.1 (1.1, 4.0)	3 (1.6, 5.7)	1.4 (0.7, 2.7)	0.4 (0.2, 0.9)
Huckleberry	1.7 (0.9, 3.3)	1.7 (0.9, 3.3)	*	1 (0.5, 2.0)	1.7 (0.9, 3.3)	12 (6.1, 23.4)
Horsetail	1.3 (0.7, 2.4)	1.3 (0.7, 2.4)	1.3 (0.7, 2.4)	0.3 (0.2, 0.5)	0.3 (0.2, 0.5)	0.4 (0.2, 0.7)
Cow parsnip	0.7 (0.3, 1.8)	*	0.7 (0.3, 1.8)	0.7 (0.3, 1.8)	2.7 (1.3, 5.7)	8.7 (4.2, 17.8)
Clover	*	45 (19, 105)	5.7 (2.6, 12.6)	17.5 (7.9, 38.6)	1 (0.4, 2.6)	*
Ants	5.7 (2.6, 12.6)	5.7 (2.6, 12.6)	45 (19.1, 105)	8.3 (3.8, 18.3)	8.3 (3.8, 18.3)	1 (0.4, 2.6)

age-classes. This result is consistent with previous studies which found blueberry and lingonberry to be sensitive to recent harvesting events (Haeussler et al., 1999; Roberts and Zhu, 2002; Nielsen et al., 2004c), likely resulting in destroyed rhizomes (Zager et al., 1983). Clover and dandelion of the young age-class were more likely to occur in post-harvest stands, similar to previous studies showing favorable responses of these exotic species to harvesting (Haeussler et al., 1999; Roberts and Zhu, 2002; Nielsen et al., 2004c). Among critical foods consumed by grizzly bears (McLellan and Hovey, 1995; Nielsen et al., 2004c; Munro et al., 2006), buffaloberry and huckleberry had greater occurrence in the mid age-class of post-fire and post-harvest stands, respectively. Soil scarification has been suggested to negatively affect the occurrence and abundance of buffaloberry (Knight, 1999; Nielsen et al., 2004c), which may partially account for the absence in the very young age-class of post-harvest stands and the greater occurrence in the mid age-class of post-fire stands; although Hamer (1996) showed that fruit production was negatively associated with forest canopy cover in 50-year old burns. Soil scarification is also speculated to destroy the rhizomes of huckleberry and thus prevent vegetative propagation, especially for recent (< 25 years) harvesting events (Martin, 1983). We suspect, however, that the effect of soil scarification on huckleberry in post-harvest stands may be negligible following sufficient forest recovery (e.g. 60 years), as can be seen when comparing post-harvest stands to mature forests alone (Table 3). Overall, ants had higher frequency of occurrence in post-fire stands in each of the three age-classes, and similarly, in post-harvest stands of the very young and young age-classes when compared to mature forests alone (Table 3). This is consistent with previous studies showing the favorable response of ants to fire and harvesting in temperate forests (Punttila et al., 1991; Nielsen et al., 2004c; Palladini et al., 2007).

Among both post-harvest and post-fire disturbances, fruit productivity was often highest among *Vaccinium* spp. Previous studies, looking at fruit productivity in coniferous stands, have also reported high productivity levels of *Vaccinium* spp. (Noyce and Coy, 1990; Nielsen et al., 2004c; Larsen et al., 2019). When comparing between disturbances, fruit production was highest in the very young and young age-classes of post-harvest stands, whereas for the mid age-class, productivity was highest in post-fire stands. The general pattern among both disturbances saw productivity peak in the young age-class, while falling sharply in the mid age-class. Although, differences in digestible energy from fruits between the two disturbances were less noticeable in the young age-class; this may be due in part to post-fire stands sampled in this study having a higher proportion of fruit from relatively energy-rich species compared to post-harvest stands. Our digestible energy results from fruits support our hypothesis that post-harvest and post-fire stands are not different from one another when considering fruit species important to grizzly bears. However, differences between age-classes were evident, with the mid age-class being significantly different from the young age-class, thus supporting our age-class hypothesis here.

Finally, fruit productivity and digestible energy in the very young age-class is comparatively smaller in the post-fire stands. This may be influenced by fire severity, where plant succession can be hindered following a severe fire. However, we were unable to account for fire severity in our analysis as reliable data were not available.

In contrast to fruit productivity, forb productivity was highest among the very young age-class, which indicated the proliferation of exotic (clover and dandelion) and early-successional (horsetail) species following a disturbance. Among all three age-classes, forb productivity was highest in post-fire stands, with large differences in productivity between disturbances in the young age-class. The proliferation of early-successional species is typical following a disturbance, as increased exposure to sunlight and extreme temperatures favor plant communities dominated by annual and shade-intolerant herbaceous species (Swanson et al., 2011). Low forb productivity in the young age-class of post-harvest stands may stem from a combination of canopy closure following succession and herbicide application frequently used in the timber industry to encourage growth of economically valuable coniferous species (Thompson and Pitt, 2011). Our digestible energy results from forbs do not support our hypothesis that post-harvest and post-fire stands are not different from one another, whereas our results do support that there were differences between age-classes, thus only supporting our age-class hypothesis here. Differences between age-classes were evident, with most of the variation in age-class covariate explained by the mid age-class.

When considering total available digestible energy, our results support our hypotheses that there were no differences between post-harvest and post-fire stands and that there were differences between age-classes, with most variation in the age-class covariate explained by the mid age-class. When adjusting total available digestible energy in the upper foothills of our study area, there was considerably more total energy available in very young and young age-classes of post-harvest stands, while the opposite pattern was observed in the mid age-class of post-fire stands. This can have important implications for grizzly bear conservation as grizzly bears are known to frequent relatively recent disturbances (Nielsen et al., 2004a; Kearney et al., 2019). In our study area, the amount of total available digestible energy in post-harvest stands, and comparatively little in post-fire stands, suggests some form of continued disturbance from forestry practices may benefit grizzly bears if access management can be controlled. We further suspect that this pattern would hold even when considering digestible energy derived from meat sources, as ungulates are known to make extensive use of areas recently (< 25 yrs) disturbed by forestry and/or wildfire (Fisher and Wilkinson, 2005). This suggests that harvested areas could be used as a management tool to boost population recovery efforts and increase population sizes, by enhancing food- and habitat-supply for a threatened grizzly bear population in a fire-suppressed landscape, so long as human access (source of mortality) is managed.

Differences in energy between harvested areas and areas disturbed

by fire may be inflated, especially for the very young and young age-classes. The lack of relatively young post-fire stands suggests that the occurrence and distribution of forest fires in our study area may not be entirely natural, in the sense that recent wildfires are more likely to be suppressed (Johnson et al., 2001; Cumming, 2005). This conceivably results in an overrepresentation of relatively young post-fire stands moderated by fire suppression, relative to stands in which wildfire is allowed to burn largely in the absence of human influence. Furthermore, because of fire suppression, changing fire regimes in the region has contributed towards forest stands dominated by coniferous species (Rhemtulla et al., 2002), which are of high timber value. As such, fire-suppressed areas that historically would have produced productive early seral burns following a natural wildfire disturbance are now favored by the timber industry for harvesting. This leaves natural wildfires to occur more frequently in areas not historically predisposed to fire disturbance, thus further contributing to an overrepresentation of relatively young post-fire stands of lower habitat quality, specifically as it relates to plant foods consumed by grizzly bears. We speculate that this may contribute to how differences in digestible energy between both disturbances are interpreted in this study, as field observations indicated that some post-fire plots sampled in this study occurred in areas of fire suppression. Further studies may consider comparing harvested areas to areas disturbed by natural wildlife alone (i.e. not fire-suppressed) to better understand differences between disturbance types.

5. Conclusion

Both recent forest harvests and fire disturbances in the foothills of west-central Alberta increase the availability of grizzly bear foods. We suggest that current and future forestry disturbances may act as a surrogate for wildfires in a fire-suppressed landscape, and thus serve as a management tool for maintaining or enhancing grizzly bear food supply. This may therefore contribute to population recovery efforts, especially in fire-suppressed areas. However, control of human access is still needed, as productive bear habitats in areas of increased road access can be associated with increases in human-caused mortality

Appendix A

See Tables A1 to A3

Table A1

Literature sources of fruit dry mass and digestible energy for various species and food categories.

Species	Fruit Dry Mass (gram)	Source
Black twinberry	0.042	Ehrlén and Eriksson, 1991; White et al., 2005
Currant	0.053	Piper, 1986; López-Alfaro et al., 2015
Gooseberry	0.053	Piper, 1986; López-Alfaro et al., 2015
Buffaloberry	0.024	Coogan et al., 2014, Supporting Information Table 11
Lowbush cranberry	0.04	Traveset et al., 2004
Bearberry	0.08	Traveset et al., 2004
Strawberry	0.023	Revegetation Species Profiles, 2013
Raspberry	0.357	Jolliffe, 1975a,b (fresh weight); Ehrlén and Eriksson, 1991
Dwarf bilberry	0.035	Nielsen et al., 2004
Huckleberry	0.035	Nielsen et al., 2004
Blueberry	0.039	Coogan, 2012, Table A3
Lingonberry	0.035	Coogan, 2012, Table A3; Ehrlén and Eriksson, 1991
Food Category	Digestible Energy (Kcal/gram_dry mass)	Source
Fruit	2.6	López-Alfaro et al., 2015, Table 2
Vegetation Summer	1.6	López-Alfaro et al., 2015, Table 2

(Nielsen et al., 2004b; Boulanger and Stenhouse, 2014), which could create trap-like conditions as an attractive habitat becomes a sink (Nielsen et al., 2006; Northrup et al., 2012; Lamb et al., 2016). Fire activity in the boreal forest is anticipated to increase under climate change (Flannigan et al., 2009). Under these conditions, persistent fire management and response will likely lead to continued fire suppression. Thus, a future fire-suppressed landscape denuded of relatively young post-fire stands may favor some form of continued disturbance (e.g. forest harvesting) that is similar to wildfire disturbance, especially as it relates to grizzly bear food supply. However, wildfires suppression is already reaching its peak effectiveness, and small increases in wildfire occurrence can lead to a disproportionate increase in wildfires (Podur and Wotton, 2010). Furthermore, there has been a move towards allowing more wildfires to burn on the landscape to maintain ecological processes (Coogan et al., 2019). Thus, forestry harvest practices to maintain grizzly bear food- and habitat-supply may not be as necessary under more active future fire regimes.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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, ConocoPhillips, Seven Generations Energy, Shell Canada, TransCanada Pipelines, Teck Resources, Talisman Energy, West Fraser, Westmoreland Coal, and Weyerhaeuser. More information can be found at <http://paw.forestry.ubc.ca/>. We would like to thank Victoria Masquillier for assistance in the field. We also thank Colleen Cassidy St. Clair and two anonymous reviewers whose insightful comments improved the quality of this manuscript. The authors declare no competing interests exist.

Table A2

Estimated odds ratios and 95% confidence intervals describing the occurrence of 18 grizzly bear food items between post-harvest and post-fire stands by age-class. Refer to Fig. 2 for visual representation.

Grizzly bear food item		Age-class		
Category	Species Name	Very Young	Young	Mid
Shrub-fruit	Black twinberry	2.1 (1.2, 3.7)	2.22 (1.2, 4.0)	1.46 (0.8, 2.6)
	Currant	4.67 (2.6, 8.5)	0.45 (0.2, 0.8)	1.68 (0.9, 3.3)
	Gooseberry	NA	1.68 (0.9, 3.3)	1 (0.6, 1.7)
	Buffaloberry	NA	1.46 (0.8, 2.6)	0.27 (0.1, 0.6)
	Lowbush cranberry	4.67 (2.6, 8.5)	1.46 (0.8, 2.6)	7.11 (3.8, 13.2)
	Western mountain-ash	NA	2.22 (0.9, 5.2)	3.75 (2, 7.1)
Dwarf shrub-fruit	Bearberry	NA	12 (5.4, 26.3)	NA
	Strawberry	7.89 (4.1, 15.1)	0.66 (0.4, 1.2)	1.52 (0.8, 2.8)
	Raspberry	8.33 (3.8, 18.3)	1 (0.5, 1.9)	1 (0.6, 1.7)
	Dwarf bilberry	0.69 (0.4, 1.2)	7.11 (3.8, 13.2)	0.27 (0.1, 0.5)
	Huckleberry	1 (0.5, 1.9)	NA	7.11 (3.8, 13.2)
	Blueberry	0.19 (0.1, 0.4)	0.59 (0.3, 1.2)	1.46 (0.8, 2.6)
	Lingonberry	1 (0.6, 1.8)	0.18 (0.1, 0.4)	0.48 (0.3, 0.8)
	Horsetail	1 (0.5, 1.9)	0.21 (0.1, 0.4)	1.46 (0.8, 2.6)
Forb/Ants	Cow parsnip	NA	1 (0.4, 2.6)	3.18 (1.8, 5.8)
	Dandelion	17.45 (7.9, 38.6)	5.38 (2.8, 10.2)	NA
	Clover	NA	3.06 (1.7, 5.4)	NA
	Ants	1 (0.6, 1.8)	0.19 (0.1, 0.4)	0.12 (0.1, 0.3)

Table A3

The average berry density of shrub-fruit (plant height ≥ 50 cm) and dwarf-shrub fruit (plant height < 50 cm) categories, and the average stem density of forbs, on a per hectare basis for 17 grizzly bear food items in post-harvest, post-fire, and mature forests. Abundance estimates for ants are absent as this was not recorded in this study. Age-class categories are as follows: Very Young (VY); Young (Y); and Mid (M).

Category	Species Name	Age-class	Harvest	SE	Fire	SE	Mature forests	SE
Shrub-fruit	Black twinberry	VY	3330	2000	50	NA ^a	140	70
		Y	180	100	850	610		
		M	0	NA	140	90		
	Currant	VY	50	NA ^a	0	NA	0	NA
		Y	0	NA	3860	2840		
		M	0	NA	0	NA		
	Gooseberry	VY	190	130	360	250	1410	640
		Y	1660	650	1780	990		
		M	3480	3200	800	670		
	Buffaloberry	VY	0	NA	0	NA	1010	520
		Y	9670	8800	0	NA		
		M	0	NA	0	NA		
Lowbush cranberry	VY	530	300	80	60	220	100	
	Y	260	120	330	190			
	M	110	60	0	NA			
Western mountain-ash	VY	0	NA	0	NA	0	NA	
	Y	0	NA	0	NA			
	M	0	NA	0	NA			
Dwarf shrub-fruit	Bearberry	VY	0	NA	0	NA	0	NA
		Y	910	NA ^a	0	NA		
		M	0	NA	1640	NA ^a		
	Strawberry	VY	2000	NA ^a	0	NA	0	NA
		Y	730	NA ^a	0	NA		
		M	180	NA ^a	0	NA		
	Raspberry	VY	15270	8020	1090	NA ^a	120	80
		Y	6180	5040	18550	16790		
		M	180	NA ^a	3270	2340		
	Dwarf bilberry	VY	89270	50710	180	NA ^a	0	NA
		Y	306910	182210	0	NA		
		M	360	NA	0	NA		
	Huckleberry	VY	51460	NA ^a	360	NA ^a	1090	NA ^a
		Y	0	NA	0	NA		
		M	360	244	0	NA		
	Blueberry	VY	9640	6530	25270	21800	790	560
		Y	31460	NA ^a	84180	82200		
		M	18910	16480	12000	NA ^a		
Lingonberry	VY	26000	25600	0	NA	4360	2330	
	Y	12000	11410	50180	40950			
	M	3640	NA ^a	36180	30510			

(continued on next page)

Table A3 (continued)

Category	Species Name	Age-class	Harvest	SE	Fire	SE	Mature forests	SE
Forb	Horsetail	VY	133460	60950	228730	68820	118120	27950
		Y	2730	1690	188550	101010		
		M	6550	3660	12550	11560		
	Cow parsnip	VY	0	NA	0	NA	60	NA ^a
		Y	0	NA	360	NA ^a		
		M	550	390	360	NA ^a		
	Dandelion	VY	18730	9940	0	NA	0	NA
		Y	4180	3310	0	NA		
		M	0	NA	0	NA		
	Clover	VY	18360	15280	180	NA ^a	0	NA
		Y	11090	10500	180	NA ^a		
		M	0	NA	0	NA		

^a – recorded only single observation.

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