ARTICLE

Wildfire extends the shelf life of elk nutritional resources regardless of fire severity

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Abstract

Large-scale, high-severity wildfires are increasingly frequent across the western United States. Fire severity affects the amount of vegetation removed and helps dictate what, where, and how many plants regenerate postfire, potentially altering the available habitat and nutritional landscape for wildlife. To evaluate the effects of fire severity on summer nutritional resources for elk (*Cervus canadensis*), we collected field data and remotely sensed information in Years 2 and 3 after a large-scale wildfire to compare forage quality and quantity across forest types and fire severities within the summer range of one elk population in west-central Montana. To understand the landscape-level effects of fire severity on nutritional resources, we developed predictive forage quality and quantity models. We used these models to predict nutritional resources across the landscape for four landscape scenarios representing different fire severity patterns (i.e., an unburned landscape, a landscape burned only at low severity, a landscape burned only at high severity, and the observed landscape burned at mixed severity). Shortly after the wildfire, summer forage quality and herbaceous forage quantity increased in both burned mesic and dry mixed-conifer forests regardless of fire severity. Summer shrub forage quantity was greater in unburned mesic and dry forests, and there was no difference between fire severities in dry forests. Low-severity burned mesic forests had significantly greater shrub forage quantity compared with high-severity burned mesic forests. The three predicted burned landscape scenarios had the highest percentage of the summer range with adequate forage quality, which increased throughout the summer. By contrast, the predicted unburned landscape had the lowest percentage of summer range with adequate forage quality, which decreased throughout the summer. Wildfire extended the duration in which elk can access high-quality forage in the summer in Years 2 and 3 postfire. Therefore, shortly after a large-scale wildfire, elk may be better able to meet their nutritional requirements, which may positively impact elk body condition, reproductive performance, and survival.

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INTRODUCTION

In recent decades, wildfires have increased in both frequency and severity across the western United States (Dennison et al., 2014; Flannigan et al., 2013; Parks & Abatzoglou, 2020; Westerling, 2016). In the central Rocky Mountain region, recent wildfires have burned nearly double the amount of the total area since the 1980s (Higuera et al., 2021). These trends are projected to continue under a changing climate, leading to substantial ecological impacts (Barbero et al., 2015; Flannigan et al., 2013; Littell et al., 2010; Stavros et al., 2014). In conifer-dominated forest ecosystems, wildfires transition forests to early successional stages and thus play a crucial role in shaping forest structure and composition (Adams, 2013). These changes in vegetative structure, therefore, alter wildlife habitat through changing the availability and dispersion of nutritional and cover resources. Wildlife responds to these disturbances to meet survival and reproductive requirements, potentially influencing both demography and distributions after a wildfire (Hebblewhite et al., 2009; Kotliar et al., 2008; Roberts et al., 2015; Saab & Vierling, 2001). Fire severity is a key component of wildfires with variable effects on vegetation and, therefore, potentially wildlife habitat. However, the impact of fire on wildlife has frequently been treated as binary (i.e., burned vs. unburned), and a deeper understanding of the effect of fire severity on habitat is needed to inform management of wildlife against a backdrop of burned forests (Fontaine & Kennedy, 2012; Geary et al., 2020; Volkmann et al., 2020).

Understanding the summer nutritional landscape postfire may provide insight into elk (*Cervus canadensis*) population dynamics. For elk, nutritional resources are a key factor affecting adult female survival, reproduction, and juvenile recruitment (Cook et al., 2004, 2013; Parker et al., 2009), yet research has not addressed the impacts of wildfire severity on elk forage quality and quantity. Nutritional demands for female elk vary seasonally and depend upon pregnancy status, lactation status, and winter weather conditions (Cook et al., 2004, 2013; Parker et al., 2009). The highest energetic costs for female elk are incurred from late winter, when energy requirements increase during the final trimester of gestation (Pekins et al., 1998), through the summer months during lactation (Cook et al., 2004). Thus, the nutritional resources available during summer play an integral role in determining the body condition of the female year-round, influencing pregnancy rates in the fall, overwinter survival, and neonatal birth mass and survival (Cook et al., 2004; Parker et al., 2009; Proffitt et al., 2016), which, in turn, can affect elk population numbers (Gaillard et al., 2000).

Knowledge on how wildfires alter the spatial and temporal availability of forage quality and quantity in the summer may provide insight into understanding elk distributions postfire. Nutrition is a combination of forage quality (i.e., nutrient composition) and quantity (i.e., food abundance) and foraging behavior (Cook et al., 2016; Pretorius et al., 2011). At a larger scale, elk select for foraging habitats across the landscape, and at a smaller scale, elk select for plants within plant communities. Elk alter their selection of nutritional resources dependent upon seasonal requirements and spatiotemporal availability. In summer, elk respond to spatial variation in nutritional resources by typically selecting foraging areas with open tree canopy to access high-quality forage (Boyce et al., 2003; Rowland et al., 2018; Skovlin et al., 2002). Elk, also, respond to temporal variation in nutrition, driven by plant phenology (Hebblewhite et al., 2008). As plants age and become more fibrous, the nutritional quality decreases because gut passage time is increased and digestibility is reduced (Spalinger & Hobbs, 1992; Van Soest, 1982). Therefore, elk select high-quality forage to maximize nutrient intake to meet nutritional demands.

Elk demography and distributions are linked to the distribution and availability of nutritional resources. Fire strongly impacts nutritional resources, although effects are dependent on time since fire (Proffitt et al., 2019; Van Dyke & Darragh, 2006) and prefire plant communities (Proffitt et al., 2019; Sachro et al., 2005) and vary in impact on digestibility and duration. In general, ungulate nutritional resources have been shown to increase after a wildfire. Fire removes dead litter and woody vegetation in the understory and opens the canopy. Therefore, more sunlight can reach the forest floor allowing for higher quality and quantities of forage to flourish (i.e., forbs and graminoids; Cook et al., 1994; Merrill et al., 1980; Sachro et al., 2005; Tracy & McNaughton, 1997). Time since fire plays an important role in determining nutritional resource availability. Typically, more recently burned areas have higher forage quality and variable forage quantity depending on vegetation type prefire (Proffitt

et al., 2019; Van Dyke & Darragh, 2006). However, the duration of postfire nutritional resource increase has also varied from a range of no change to several decades likely due to site-specific differences (Cook et al., 2016; Hobbs & Spowart, 1984; Pearson et al., 1995; Proffitt et al., 2019). Additionally, season (Hobbs & Spowart, 1984; Proffitt et al., 2019) and landscape features such as elevation (Greene et al., 2012; Proffitt et al., 2019) and aspect (Greene et al., 2012) affect how nutritional resources are impacted by fire.

Wildfire severity may be another source of postfire variation in nutritional resources. Wildfire severity is an important component of large-scale wildfires that differentially influences vegetation communities, and therefore, potentially nutrition, across the landscape. For example, low-severity burned forests have been shown to have higher graminoid, shrub, and forb cover compared to high-severity burned forests shortly after a wildfire (Turner et al., 1997), potentially leading to differences in herbaceous and shrub forage quantity for elk. Additionally, the composition and phenology of the plant community may differ between fire severities because of variation in regeneration strategies (Heinselman, 1981; Turner et al., 1997) and microclimate (Stevens et al., 2015; Wolf et al., 2021) potentially leading to differences in forage quality. For example, the greater sun exposure in high-severity burned forests could lead to earlier vegetation senescence, and therefore, lower forage quality compared with low-severity burned forests where the canopy cover remains partially intact. These differences between fire severity classes are likely to become less pronounced as time since fire increases and the canopy cover closes. However, shortly after a fire, these potential differences in plant cover, composition, and phenology suggest that fire severity could play an important role in determining forage quality and quantity for elk.

Although knowledge on the effects of fire on elk nutrition is increasing, it is important to understand the impacts of fire severity because potentially small differences in the spatiotemporal availability of nutritional resources could lead to changes in reproductive performance and survival (Cook et al., 2004). As large-scale and high-severity fires continue to increase in frequency, understanding the postfire nutritional landscape through incorporating fire severity will be important for future wildlife management. To address this gap, our objective was to evaluate the effects of low- and high-severity fire on elk summer forage quality and quantity in Years 2 and 3 after a large-scale wildfire in west-central Montana. We hypothesized that fire severity variably affects summer forage quality and quantity dependent upon forest type (i.e., mesic vs. dry conifer forests). We predicted that forage quality would be lowest in unburned forests,

highest in low-severity burned forests, and moderate in high-severity burned forests. For herbaceous forage biomass, we predicted that biomass would be lowest in unburned forests, highest in low-severity burned forests, and moderate in high-severity burned forests. Lastly, we predicted that shrub forage biomass would be highest in unburned forests, moderate in low-severity burned forests, and lowest in high-severity burned forests.

METHODS

Study area

The study was conducted in west-central Montana in the Ovando–Seeley Lake area and focused on the summer range of the Blackfoot–Clearwater (BC) elk population (Figure 1a). The BC elk population was estimated at approximately 1000 animals between 2018 and 2020 based upon aerial surveys. We calculated the 95% kernel density estimate to determine the population-level summer range (15 May–31 August) from 53 adult female elk that were captured and GPS collared using helicopter net gunning or chemical immobilization in accordance with animal welfare protocols approved by Montana Fish, Wildlife, and Parks (IACUC number FWP13-2018). Approximately 40% of the 1247-km^2 elk population's summer range was impacted by the Rice Ridge Fire, which started due to a lightning strike on 24 July 2017 and continued to burn through 7 September 2017. The approximately 623-km^2 mixed-severity fire included approximately 46% low-severity and 54% high-severity burns (Figure 1b).

Prefire forest communities were dominated by Rocky Mountain Subalpine Dry-Mesic Spruce-Fir Forest and Woodland, further referred to as mesic forests, with the dominate conifers being Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Rocky Mountain Dry-Mesic Montane Mixed-Conifer Forest, further referred to as dry forests, also made up a large portion of the study area, and these forests were dominated by lodgepole pine (*Pinus contorta*), western larch (*Larix occidentalis*), Douglas fir (*Pseudotsuga menziesii*), and ponderosa pine (*Pinus ponderosa*). Within the summer range, mesic and dry forests comprised 71.5% of the landscape where 53%, 21%, and 26% were classified as unburned, low severity, and high severity, respectively (Appendix S1: Table S2). The habitats at lower elevation included irrigated agriculture, cattle grazed pastures, riparian areas, deciduous shrublands, and montane grasslands dominated by bluebunch wheatgrass (*Pseudoroegneria spicata*), rough fescue (*Festuca campestris*), or Idaho fescue (*Festuca idahoensis*). Elevation ranged from 1150 to
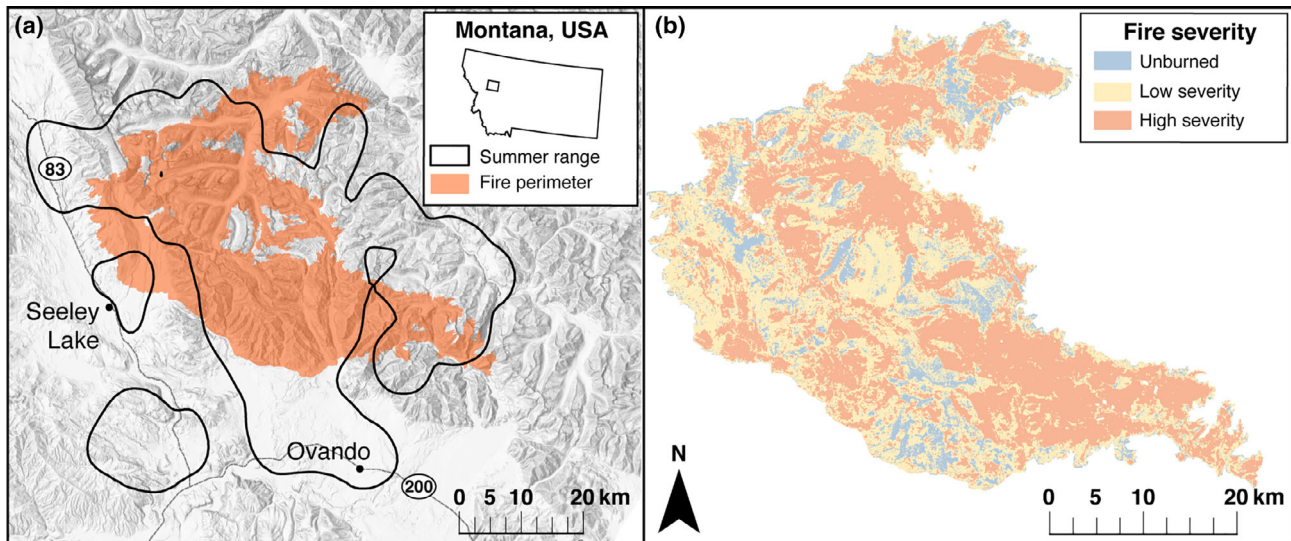
FIGURE 1 The Blackfoot–Clearwater elk population summer range and the perimeter of the Rice Ridge Wildfire located in the Ovando–Seeley Lake area of west-central Montana, USA (a), and the fire severity burn pattern from the wildfire (b).

2600 m with varied topography including flat bottomland, foothills, and steep and rugged mountain slopes. Annual precipitation ranged from 380 mm in valley bottoms to 1500 mm in the mountains with most precipitation falling as snow in the winter, and mean temperatures for July and January were 17.22 and −6.1°C, respectively (Prism Climate Group).

Data for this study were collected during normal precipitation and temperature conditions for the study area compared to 30-year normals. Mean summer precipitation (May–August) for 2019, 2020, and the 30-year normal are 51.9 mm (SD = 12.17 mm), 65.43 mm (SD = 10.94 mm), and 56.56 mm (SD = 11.84 mm), respectively. Mean summer temperatures for 2019, 2020, and the 30-year normal are 12.42°C (SD = 1.07°C), 12.41°C (SD = 0.98°C), and 12.37°C (SD = 1.26°C), respectively.

Overview

We developed a landscape nutrition model predicting forage quality and quantity within the BC elk population summer range following similar methods as Proffitt et al. (2016, 2019). First, fecal samples were collected and DNA metabarcoding was used to determine the primary summer forage species (species from Feces-Bat Ecology and Genetics Lab, Northern Arizona University, Flagstaff, AZ, USA; Appendix S2). Next, we sampled vegetation across a gradient of fire severity and vegetation types to estimate forage quality and quantity. All sampling was conducted from May through August of 2019 and 2020, Years 2 and 3 postfire. Finally, we developed summer

landscape nutrition models that predicted forage quality and quantity as a function of spatial and temporal covariates. To understand the effects of variable fire conditions, we used the summer range boundary to estimate the availability of forage quality, herbaceous forage biomass, and shrub forage biomass available to elk within four different landscape scenarios.

Vegetation sampling sites

We selected vegetation sampling sites based on a generalized random tessellation stratified sampling approach (Stevens Jr. & Olsen, 2004) within six vegetation cover types of interest to elk. Our land cover model was developed using prefire vegetation types based on multiple land cover products (Appendix S1). Fire severity and extent for the Rice Ridge Wildfire was determined using the Rapid Assessment of Vegetation Condition after Wildfire product (RAVG; https://fsapps.nwcg.gov/ravg/; Appendix S1). The six vegetation cover types included conifer-dominated mesic forest types (dominated by subalpine fir and Engelmann spruce) and conifer-dominated dry forest types (dominated by lodgepole pine, ponderosa pine, Douglas fir, and western larch) each with three fire severity categories (unburned, low severity, and high severity). We focused our summer sampling on mesic and dry forests as they comprised greater than 70% of the vegetation cover types found within the elk population's summer range. We additionally sampled five other vegetation cover types not impacted by fire, in August only, which comprised approximately 18% of the summer range (Appendix S5).

At each vegetation sampling site, we set a 40-m transect along the contour of the slope. To estimate forage quality, at the 0-, 10-, 20-, 30-, and 40-m marks, we recorded species composition within a 1-m^2 quadrat. For each species, we recorded independent percent cover estimates and recorded phenology as emergent, flowering, fruiting, mature seed, or senescent based on the dominant phases at the sampling site. To estimate forage quantity, we embedded a 0.5-m^2 clip plot within the 1-m^2 quadrat at the 0-, 20-, and 40-m mark. We clipped all graminoids and forbs above 1 to 2 cm from the ground, and for shrubs, we clipped all leaves and soft-green stems below the 2-m mark and placed each lifeform in a separate bag. We collected all live and senesced vegetation; however, we did not include previous years' litter. We dried samples from the clip plots at 55°C for 36 h and then measured weight.

Estimating forage quality and quantity

To estimate species-specific forage quality, we collected forage species that were identified from the summer diet analysis in each of the phenological stages to determine dry matter digestibility (DMD) using sequential detergent fiber analysis (Robbins, Hanley, et al., 1987; Robbins, Mole, et al., 1987; Van Soest, 1982). We calculated digestible energy (DE), measured as kilocalories per gram of forage, from DMD (Cook et al., 2016; Appendix S3). We collected five individual plants of the same species–phenological stage and combined them into one composite forage sample. Composite forage samples included both leaves and stems as well as flowers and fruits when present. We dried samples within 10 h of collection at 55°C for 36 h and sent samples to the Wildlife Habitat and Nutrition Laboratory (Pullman, WA, USA). Because of low composite forage sample sizes, we sought to also use previously reported DE values from a nearby study area in the Bitterroot Valley in west-central Montana (Proffitt et al., 2016, 2019). To determine whether it was appropriate to use samples from outside the study area, we cross-checked for differences in DE between study area and phenological stage using a simple ANOVA (Appendix S3).

To estimate site-level forage quality, we filtered our species composition to summer forage species within each sampling site quadrat. Then, we took the forage species percent cover and divided it proportionally among the recorded phenological stages. We calculated the mean DE of the quadrat by multiplying these proportions by the phenological stage-specific DE and summed. We averaged the five quadrats to get the sampling site's mean DE (Appendix S3).

To estimate site-level forage quantity (in grams per square meter), further referred to as forage biomass or quantity, we distributed the clip plot's recorded dry weight for each lifeform (i.e., forb, graminoid, and shrub) proportionally among the species based on rescaled percent cover. Next, we filtered to forage species and summed the biomass for each lifeform. We combined graminoid and forb forage biomass together to form herbaceous forage biomass. We then averaged biomass across the three clip plots and scaled up to square meters (Appendix S3).

Because ocular estimates of percent cover for each species may vary from actual biomass, our results for forage quality and quantity should be interpreted as relative between fire severity classes rather than absolute.

Landscape modeling

We developed summer landscape nutrition models that predicted forage quality using linear models and forage quantity using zero-inflated negative binomial (ZINB) models as a function of spatial and temporal covariates. We modeled dry and mesic forests separately to understand the unique factors that impact nutrition within each forest type (Diaz et al., 1998; Hollingsworth et al., 2013). Additionally, we separately modeled herbaceous and shrub forage biomass to understand the distinct drivers that influence the amount of forage based on lifeform. Spatial covariates evaluated to predict forage quality and quantity included fire severity (unburned, low severity, and high severity), aspect, percent tree canopy cover, compound topography index, distance to unburned patch, elevation, patch size, and solar radiation. Temporal covariates included precipitation and week (Appendix S4). We standardized continuous covariates by subtracting their mean and dividing by their standard deviation, and we assumed covariates were measured without error. We screened covariates for collinearity, and we only included covariates with a Pearson's correlation coefficient <0.6.

We hypothesized that the effect of patch size and distance to unburned patches on forage quality and quantity would differ based on fire severity. Therefore, we included interaction terms to understand the effect of fire severity on patch size and distance to unburned patches (Heinselman, 1981; Turner et al., 1997). We also included an interaction term between elevation and week to account for the progression of vegetation emergence at higher elevations across the summer season. We converted our quantity measurements to an integer by multiplying by 100 to meet the assumptions of ZINB models. Our primary goal was to determine which

combination of the spatial and temporal covariates best predicted DE, herbaceous forage biomass, and shrub forage biomass in each of the forest types. We considered all subsets of plausible covariates and selected the most parsimonious model using corrected Akaike information criterion. For forage quality, we used R^2 values from the top models to assess goodness of fit, and for forage quantity, we used posterior predictive checks to assess predictive capability.

From the top forage quality models, we assessed the effects of covariates based on the sign and magnitude of standardized coefficient estimates, and we compared prediction estimates for fire severities by holding all other covariates at their mean value. From the top forage quantity models, we back-transformed coefficient estimates by exponentiating the value and compared the effects of fire severity by holding all other covariates at their average levels.

Phenological differences between fire severities

To evaluate whether vegetation in the burn was in earlier phenological stages throughout the summer, we tested for differences in phenological stage between fire severity categories using a Poisson regression. We developed a vegetation sampling site-level phenological metric for forb, graminoid, and shrub forage species as our response variable. At each vegetation sampling site, we multiplied the proportion of each species in each phenological stage by the ordinal value for each phenological stage (1 for emergent to 5 for senescent) and then averaged across forage species within each lifeform for each site. We included an interaction term between fire severity (unburned, low severity, and high severity) and month (May, June, July, and August) as a predictor variable. If phenology differed between fire severity categories, we expected 95% confidence intervals (CIs) of fire severity coefficients to not overlap within each month.

Predicted landscape-level differences between fire severities

To investigate potential effects of fire severity on the nutritional landscape, we used the unstandardized coefficient estimates from the top landscape nutrition models to predict forage quality and quantity within the Rice Ridge fire perimeter across four landscape scenarios: (1) an unburned landscape, (2) a landscape burned completely by a low-severity fire, (3) a landscape burned completely by a high-severity fire, and (4) the observed landscape impacted by mixed-severity fire. For each of the four predicted landscape scenarios, we calculated the area (in square kilometers) and percentage of the BC elk population's summer range within mesic and dry forests that meets the nutritional requirements for lactating female elk throughout the summer based on studies performed by Cook et al. (2004, 2016). We classified adequate nutrition as ≥2.75 kcal/g and inadequate nutrition as ≤2.74 kcal/g. For herbaceous and shrub forage biomass, we calculated the mean kilograms per hectare within mesic and dry forests for each predicted landscape throughout the summer.

RESULTS

Vegetation sampling sites

We collected 18 composite pellet samples for the summer, and we identified a total of 21 taxa as summer forage (Appendix S2). The summer diet was comprised of 10 forb, 7 shrub, and 4 graminoid taxa. The most common diet species within each of the respective lifeforms was fireweed (*Chamerion angustifolium*), huckleberry (*Vaccinium* sp.), and sedge (*Carex* sp.). We sampled a total of 682 vegetation sampling sites within 353 mesic forest sites (102 unburned, 113 low severity, and 138 high severity) and 329 dry forests sites (98 unburned, 105 low severity, and 126 high severity). The most common forage taxa at a vegetation sampling site varied within mesic and dry forests and fire severity (Figure 2).

Estimating forage quality and quantity

Median summer DE from the vegetation sampling sites was 3.00 kcal/g (25–75% quantiles: 2.65–3.22) and varied by fire severity, vegetation cover type, and month (Figure 3). Median DE for both dry and mesic forests burned by low severity (3.04 and 3.03 kcal/g, respectively) and high severity (2.98 and 2.91 kcal/g, respectively) was higher compared with unburned forests (2.75 and 2.59 kcal/g, respectively).

Median summer herbaceous and shrub forage biomass from the vegetation plot sampling was 7.96 g/m^2 (25–75% quantiles: 0.2–27.21) and 0.00 g/m^2 (25–75% quantiles: 0.00–5.66), respectively, and varied based on fire severity, vegetation cover type, and month (Figure 4). Median herbaceous forage biomass for both dry and mesic forests burned by low severity (21.4 and 12.5 g/m^2, respectively) and high severity (9.89 and 7.83 g/m^2, respectively) was higher than unburned forests (2.93 and 0.00 g/m^2, respectively). Median shrub forage biomass
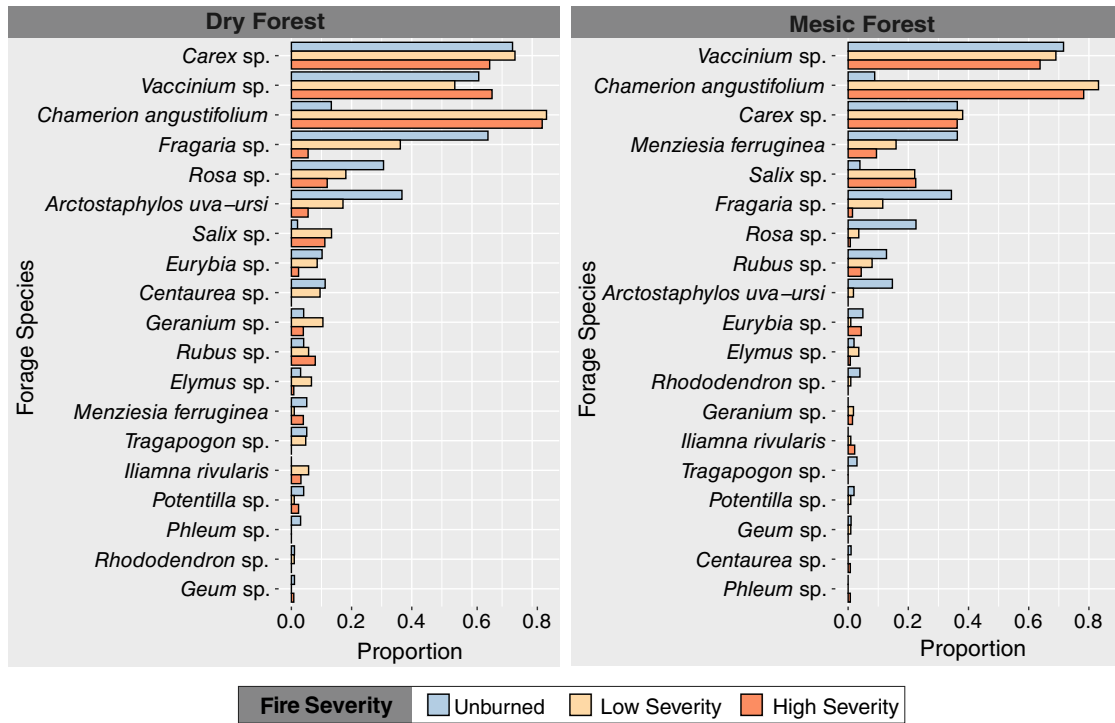
FIGURE 2 Proportion of vegetation sampling plots containing each forage species within each fire severity category in dry and mesic forests in the Blackfoot–Clearwater elk summer range in west-central Montana for 2019–2020.
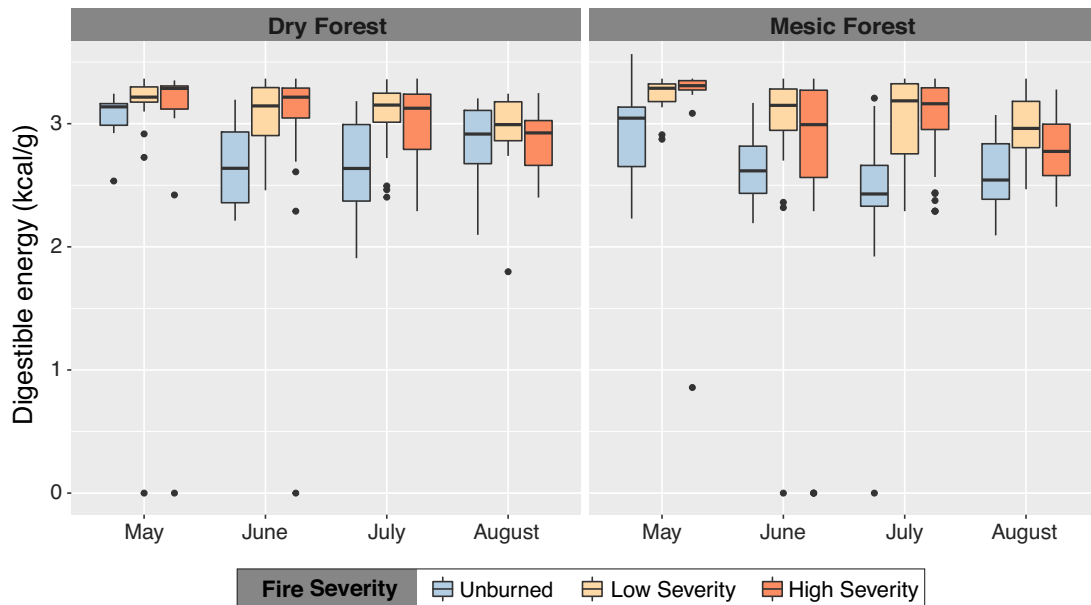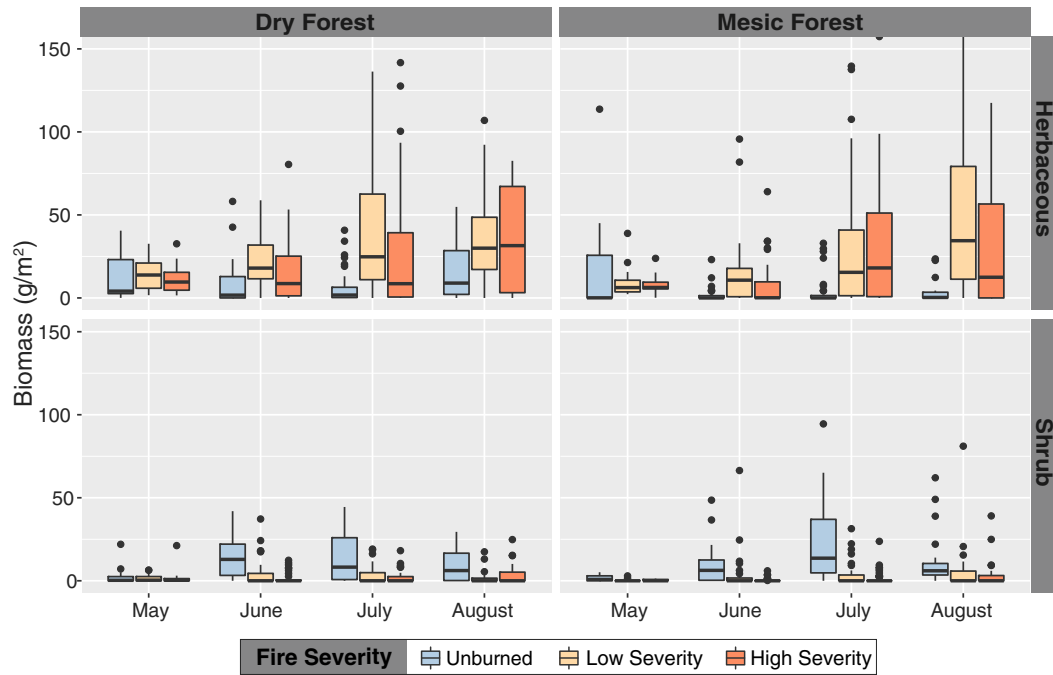

FIGURE 3 Median digestible energy measured within each vegetation cover class and month from the vegetation sampling sites (focused on summer forage species) in the Blackfoot–Clearwater elk summer range in west-central Montana for 2019–2020. The median is represented by the horizontal lines through the boxes, the interquartile range (IQR) is represented by the length of the box, 1.5 times the IQR is represented by the whiskers, and outliers >1.5 times the IQR are represented by the points outside of the whiskers.

for both dry and mesic forests was higher in unburned forests (7.15 and 6.06 g/m^2, respectively) than for forests burned by both low and high severity (0.00 g/m^2 for all burned forests).

Landscape modeling

Within dry forests, the top model predicting forage quality included the covariates fire severity, percent tree

FIGURE 4 Summer median herbaceous and shrub forage biomass (in grams per square meter) measured within each vegetation cover class and month (focused on the summer forage species) in the Blackfoot–Clearwater elk summer range in west-central Montana for 2019–2020. The median is represented by the horizontal lines through the boxes, the interquartile range (IQR) is represented by the length of the box, 1.5 times the IQR is represented by the whiskers, and outliers >1.5 times the IQR are represented by the points outside of the whiskers.

canopy cover, slope, solar radiation, and the interaction between week and elevation (R^2_{adj} = 0.16; Table 1). Forage quality in low- and high-severity forests was 7.9% (95% CI: 2.9–12.6) and 7.6% (2.1–12.9) higher than in unburned forests, respectively. There was no difference in forage quality between low- and high-severity burned forests, as confidence intervals between fire severities overlapped. Digestible energy decreased by 2.2% (95% CI: 0.1–4.5) for every standard deviation increase in percent tree canopy cover, decreased by 2.2% (95% CI: 0.5–4) for every standard deviation increase in solar radiation, and increased by 3.9% (95% CI: 2.2–6.1) for every standard deviation increase in slope. In May, DE decreased by 6.5% (95% CI: 4.3–9.0) for every standard deviation increase in elevation, but as time progressed, DE increased with elevation by 2.2% (95% CI: 0.4–4).

Within mesic forests, the top model predicting forage quality included the covariates fire severity, monthly precipitation, and the interaction term of week and elevation and their main effects (R^2_{adj} = 0.21; Table 1). Forage quality in low-severity burned forests was 16.3% (95% CI: 11.8–20.1) greater than unburned forests, and forage quality in high-severity burned forests was 14.1% (95% CI: 9.5–18.3) greater than unburned forests. Low-severity burned mesic forests trended to have 2% greater forage quality compared with high-severity burned mesic forests; however, confidence intervals between fire severities overlapped.

TABLE 1 Standardized coefficient estimates and standard errors for the top models predicting summer forage quality in each of the forest types in the Blackfoot–Clearwater elk summer range in west-central Montana for 2019–2020.

Covariate	Dry forests	Mesic forests
Intercept	**2.77 (0.052)**	**2.63 (0.046)**
Low severity	**0.22 (0.067)**	**0.43 (0.062)**
High severity	**0.21 (0.077)**	**0.37 (0.060)**
Elevation	**−0.18 (0.033)**	**−0.16 (0.028)**
Week	0.002 (0.025)	−0.025 (0.03)
Week × elevation	**0.061 (0.027)**	**0.093 (0.03)**
Slope	**0.11 (0.027)**	-
Canopy cover	**−0.064 (0.031)**	-
Solar radiation	**−0.060 (0.024)**	-
Monthly precipitation	-	**0.061 (0.025)**
Weekly precipitation	-	-
Aspect	-	-
CTI	-	-
Patch size × fire severity	-	-
Summer precipitation	-	-
R^2	0.16	0.21

Notes: Values in boldface denote 95% confidence intervals not containing 0. Effects of fire severity in dry and mesic forests are in relation to the reference unburned forest (intercept).

Abbreviation: CTI, compound topography index.

Digestible energy increased by 2.3% (95% CI: 0.4–4.2) for every standard deviation increase in precipitation. Digestible energy within mesic forests in May decreased by 6.1% (95% CI: 3.8–8) for every standard deviation increase in elevation, but as the time progressed, DE increased with increasing elevation by 3.4% (95% CI: 1.3–5.7).

Within dry forests, the top model predicting the presence/absence of herbaceous forage biomass (the zero-inflated part of the model) included fire severity and elevation (Table 2). The odds of low-severity and high-severity burned forests having no herbaceous forage biomass were 93% (95% CI: 72–98) and 65% (95% CI: 19–85) lower than those of unburned forests, respectively. The covariates predicting the amount of herbaceous forage biomass (the negative binomial part of the model) included fire severity, elevation, and week (Table 2). Low-severity and high-severity burned forests had 179% (95% CI: 98–291) and 145% (95% CI: 72–250) greater

TABLE 2 Standardized coefficient estimates and standard errors for the top models predicting summer herbaceous and shrub forage biomass within dry and mesic forests in the Blackfoot–Clearwater elk summer range in west-central Montana for 2019–2020.

Model component	Covariate	Herbaceous forage biomass		Shrub forage biomass	
		Dry forest	Mesic forest	Dry forest	Mesic forest
NB	Intercept	**7.077 (0.14)**	**7.34 (0.22)**	**7.37 (0.16)**	**7.26 (0.11)**
	Low severity	**1.02 (0.17)**	**0.95 (0.25)**	**−0.72 (0.20)**	**−0.43 (0.19)**
	High severity	**0.90 (0.17)**	**0.81 (0.29)**	**−0.98 (0.25)**	**−1.29 (0.20)**
	Canopy	-	**−0.25 (0.12)**	0.034 (0.11)	-
	Elevation	**−0.24 (0.086)**	**−0.35 (0.10)**	0.21 (0.11)	**0.31 (0.077)**
	Slope	-	-	**−0.24 (0.10)**	-
	Week	**0.35 (0.068)**	**0.53 (0.10)**	-	**0.49 (0.095)**
	Week × elevation	-	**0.32 (0.13)**	-	-
	Aspect	-	**0.25 (0.098)**	-	-
	CTI	-	-	-	-
	Patch size × fire severity	-	-	-	-
	Monthly precipitation	-	-	-	-
	Weekly precipitation	-	-	-	-
	Solar radiation	-	-	-	-
	Summer precipitation	-	-	-	-
ZI	Intercept	**−0.99 (0.27)**	0.11 (0.24)	−0.57 (0.30)	**−1.40 (0.25)**
	Low severity	**−2.62 (0.69)**	**−2.89 (0.42)**	**0.96 (0.36)**	**1.90 (0.32)**
	High severity	**−1.04 (0.42)**	**−1.91 (0.35)**	0.84 (0.42)	**2.39 (0.32)**
	Canopy	-	-	−0.35 (0.18)	-
	Elevation	**0.83 (0.21)**	**1.32 (0.19)**	**0.41 (0.14)**	-
	Weekly precipitation	-	-	**−0.27 (0.12)**	-
	Week	-	-	-	**−0.27 (0.13)**
	Slope	-	-	-	-
	Week × elevation	-	-	-	-
	CTI	-	-	-	-
	Aspect	-	-	-	-
	Patch size × fire severity	-	-	-	-
	Monthly precipitation	-	-	-	-
	Solar radiation	-	-	-	-
	Summer precipitation	-	-	-	-

Notes: "NB" refers to the negative binomial part of the model that estimates the amount of biomass, and "ZI" refers to the zero-inflated part of the model that estimates the presence or absence of biomass. Values in boldface denote 95% confidence intervals not containing zero. Effects of fire severity are in relation to the reference unburned forest (intercept).
Abbreviation: CTI, compound topography index.

herbaceous forage biomass compared with unburned forests, respectively. There was no significant difference in predicting the presence/absence or amount of herbaceous forage biomass between low-severity and high-severity burned forests as the confidence intervals widely overlapped.

Within mesic forests, the top model predicting the presence/absence of herbaceous forage biomass included fire severity and elevation (Table 2). There was 94% (95% CI: 87–98) and 85% (95% CI: 70–93) lower odds of low-severity and high-severity burned forests having no herbaceous forage biomass than unburned forests, respectively. The covariates predicting the amount of herbaceous forage biomass included fire severity, aspect, percent tree canopy cover, elevation, and the interaction term of week and elevation (Table 2). Low-severity and high-severity burned forests had 160% (95% CI: 58–327) and 124% (95% CI: 28–294) greater herbaceous forage biomass compared with unburned forests. There was no significant difference in predicting the presence/absence or amount of herbaceous forage biomass between low-severity and high-severity burned forests as the confidence intervals widely overlapped.

Within dry forests, the top model predicting the presence/absence of shrub forage biomass included fire severity, percent tree canopy cover, elevation, and weekly precipitation (Table 2). The odds that low-severity and high-severity burned forests had no shrub forage biomass were 161% (95% CI: 28–431) and 131% (95% CI: 2–422) higher than unburned forests, respectively. The covariates predicting the amount of shrub forage biomass included fire severity, percent tree canopy cover, elevation, and slope (Table 2). Low-severity and high-severity burned forests had 51% (95% CI: 28–67) and 62% (95% CI: 39–77) lower shrub forage biomass than unburned forests, respectively. There was no significant difference in predicting the presence/absence or amount of shrub forage biomass between low-severity and high-severity burned forests as the confidence intervals widely overlapped.

Within mesic forests, the top model predicting the presence/absence of shrub forage biomass included fire severity and week (Table 2). The odds that low-severity and high-severity burned forests had no shrub forage biomass were 572% (95% CI: 262–1148) and 993% (95% CI: 489–1927) greater compared with unburned forests, respectively. The covariates predicting the amount of shrub forage biomass included fire severity, elevation, and week (Table 2). Low-severity and high-severity burned forests had 35% (95% CI: 6–55) and 72% (95% CI: 59–81) lower shrub forage biomass than unburned forests, respectively. There was a significant difference in the amount of shrub forage biomass between low- and high-severity burned forests where low-severity burned forests had approximately 57% more shrub forage biomass than high-severity burned forests.

Phenological differences between fire severities

There were minimal differences in phenology between fire severity categories in May and June for forage species in each lifeform (Figure 5). In July, low- and high-severity
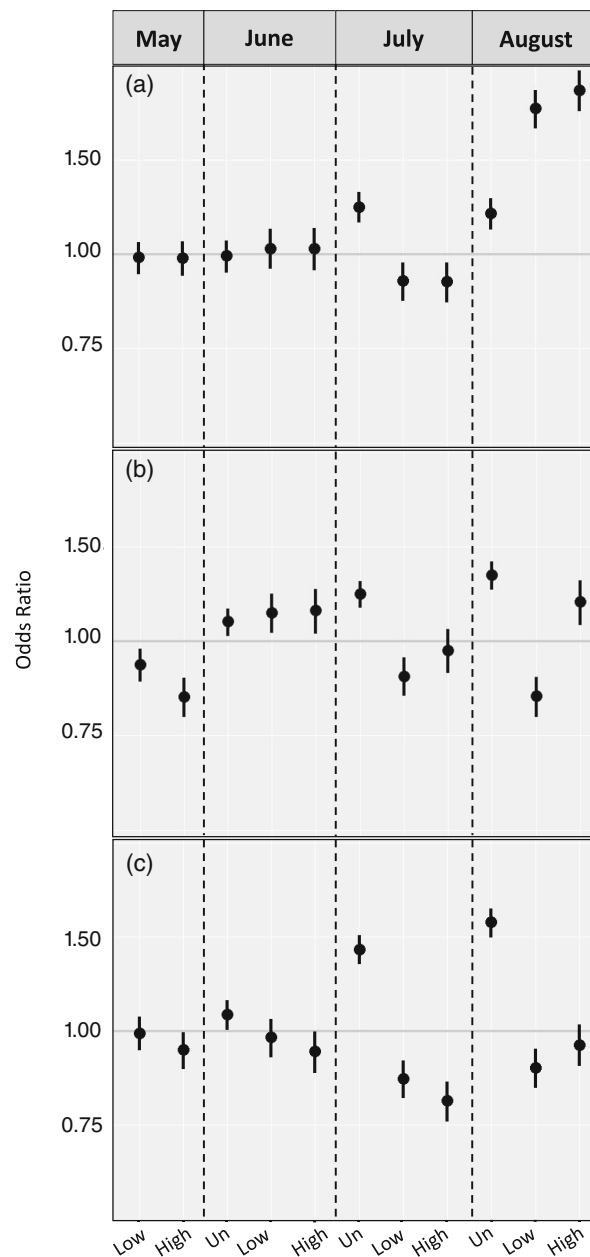
FIGURE 5 Exponentiated coefficients and 95% confidence intervals for estimating site-level phenological stage for forb (a), graminoid (b), and shrub (c) forage species as a function of fire severity and month for the Blackfoot–Clearwater elk population's summer range in west-central Montana. Anything above 1 is a later phenological stage and anything closer to or below 1 is an earlier phenological stage. The intercept is unburned forests in May, and "Un," "Low," and "High" represent unburned forests, low-severity burned forests, and high-severity burned forests, respectively.

T A B L E 3 Percentage of sampling sites in unburned, low-severity, and high-severity burned forests classified as having early phenology (emergent and flowering) in July and August for each plant lifeform in the Blackfoot–Clearwater elk summer range in west-central Montana for 2019–2020.

Fire severity	July phenology			August phenology		
	Forb	**Graminoid**	**Shrub**	**Forb**	**Graminoid**	**Shrub**
Unburned	88.90%	75.60%	79.30%	96.80%	71.40%	65.00%
Low severity	98.50%	87.50%	89.10%	57.80%	90.30%	81.60%
High severity	98.10%	90.00%	97.80%	48.10%	83.30%	82.20%

burned forests were at significantly earlier phenological stages than unburned forests for each lifeform, suggesting that forage species were continuing to emerge in July in burned forests. Approximately 10%–20% more burned sampling sites were classified as having early phenology (emergent and flowering) compared with unburned sampling sites in July (Table 3). In August, phenological differences varied as a function of lifeform and fire severity (Figure 5). For forbs, unburned forests had an earlier phenological stage compared with low- and high-severity burned forests. Unburned sampling sites had approximately 39% and 48% more sampling sites with forbs classified as early phenology compared with low- and high-severity burned forests, respectively (Table 3). For graminoids and shrubs in August, low- and high-severity burned forests had significantly earlier phenological stages compared with unburned forests. Approximately 12%–19% more burned sampling sites were classified as early phenology compared with unburned sites (Table 3).

Predicted landscape-level differences between fire severities

The percentage of the summer range with adequate DE varied based on month and landscape scenario (Figure 6). For the observed mixed-severity, low-severity, and high-severity predicted landscape scenarios, percent adequate DE generally increased during summer and did not vary substantially. In general, approximately half of the landscape had adequate DE throughout the summer for each of the predicted burned landscape scenarios. For the unburned scenario, the majority of the landscape provided inadequate DE. For the unburned predicted landscape, percent adequate DE was substantially lower than in the three predicted burned landscape scenarios, and the percent adequate DE across the summer range decreased from month to month. For example, the unburned landscape had 18%, 24%, 29%, and 36% less of the landscape with adequate DE compared with the landscape burned with the observed mixed-severity conditions from May to August, respectively (Figure 7). The

low-severity landscape had 2.9%, 4.3%, 5.0%, and 0.2% more of the landscape with adequate DE compared with a high-severity landscape in May, June, July, and August, respectively.

The mean kilograms per hectare of herbaceous and shrub forage biomass within dry and mesic forests in the summer range increased throughout the summer and varied based on fire severity scenario (Figure 6). Herbaceous forage biomass did not substantially vary across the observed mixed-severity, low-severity, and high-severity predicted landscapes but was substantially lower across each month for the unburned landscape. For example, the observed mixed-severity predicted landscape compared with the unburned predicted landscape had 66%, 68%, 41%, and 42% more herbaceous forage biomass (in kilograms per hectare) in May, June, July, and August, respectively. The low-severity predicted landscape had approximately 10% more herbaceous forage biomass compared with a high-severity predicted landscape at each time step. Shrub forage biomass for each of the four predicted landscapes was highest in the unburned landscape, and greater in the low-severity predicted landscape compared with the high-severity predicted landscape. The low-severity predicted landscape had approximately 17%, 15%, 22%, and 24% greater shrub forage biomass compared with a high-severity predicted landscape in May, June, July, and August, respectively.

DISCUSSION

Our results add to the growing body of literature showing how wildfire affects summer nutritional resources for elk in coniferous forests. Fire severity is a main component of wildfire, and our study is the first to address the effects of fire severity on elk nutritional resources at a landscape-level scale. Our results highlight that in Years 2 and 3 after a large-scale wildfire, forage quality and quantity changed during the summer as a function of landscape characteristics and vegetation cover types. We found that fire improved forage quality regardless of fire
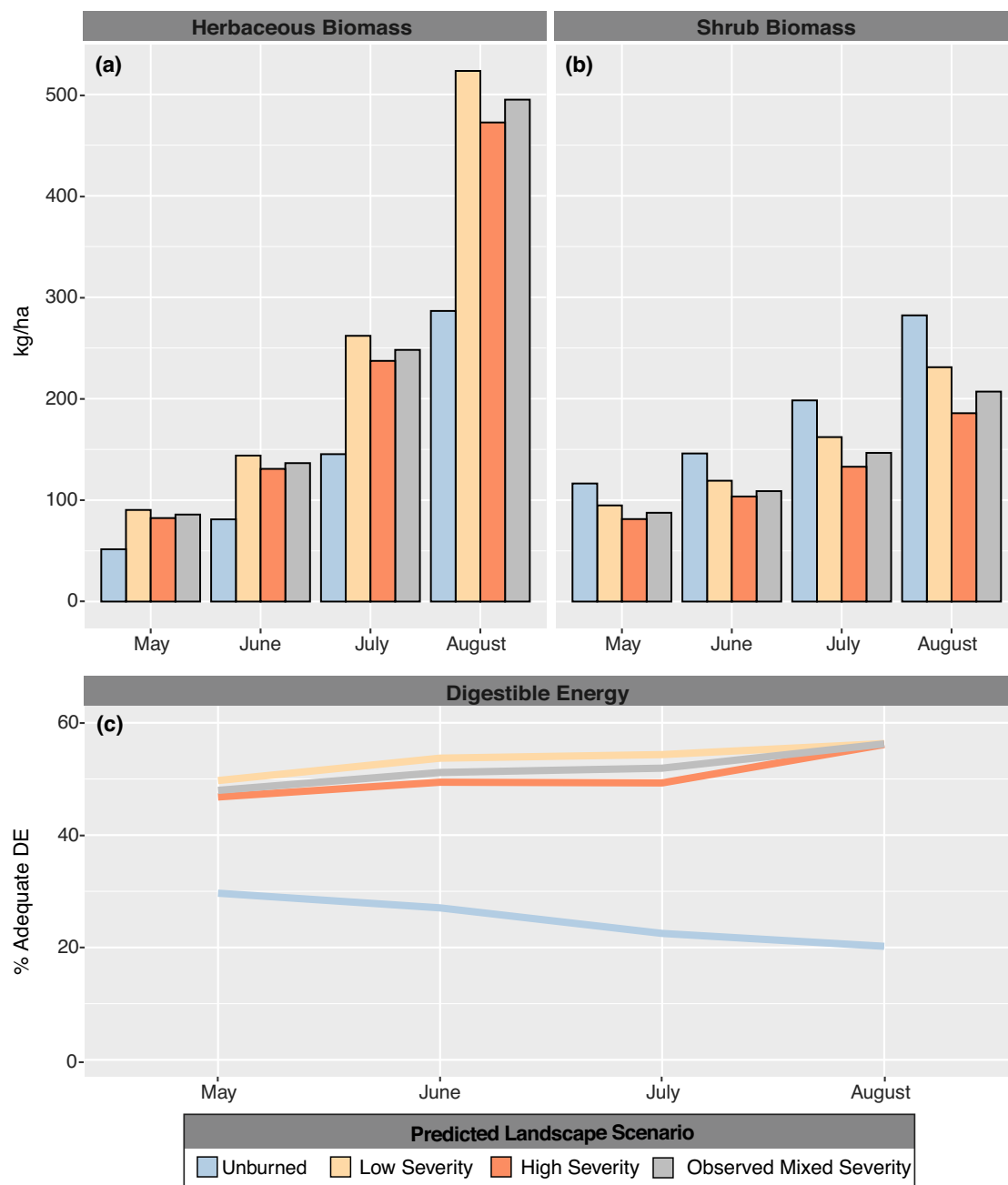
FIGURE 6 The average kilograms per hectare per month for herbaceous forage biomass (a) and shrub forage biomass (b) within the summer range of the four predicted landscape scenarios in the Blackfoot–Clearwater elk population's summer range. (c) The percentage of the Blackfoot–Clearwater elk population's summer range within the four predicted landscape scenarios that meets the threshold of >2.75 kcal/g of forage to be considered adequate for each month.

severity and that fire severity had variable effects on forage quantity dependent upon forage type and forest type. Fire, in conjunction with spatiotemporal factors, potentially altered the availability and distribution of forage for elk by extending the duration in which elk could access high-quality forage throughout the summer. These results have strong implications for management, as changes in the nutritional landscape could potentially lead to changes in female elk body condition, demography, and distributions.

Our results supported our hypothesis that fire improved forage quality in both mesic and dry forests in Years 2 and 3 postfire, but we did not find evidence that there was a significant difference in forage quality between low- and high-severity burned forests. Higher forage quality within burned forests may be explained by
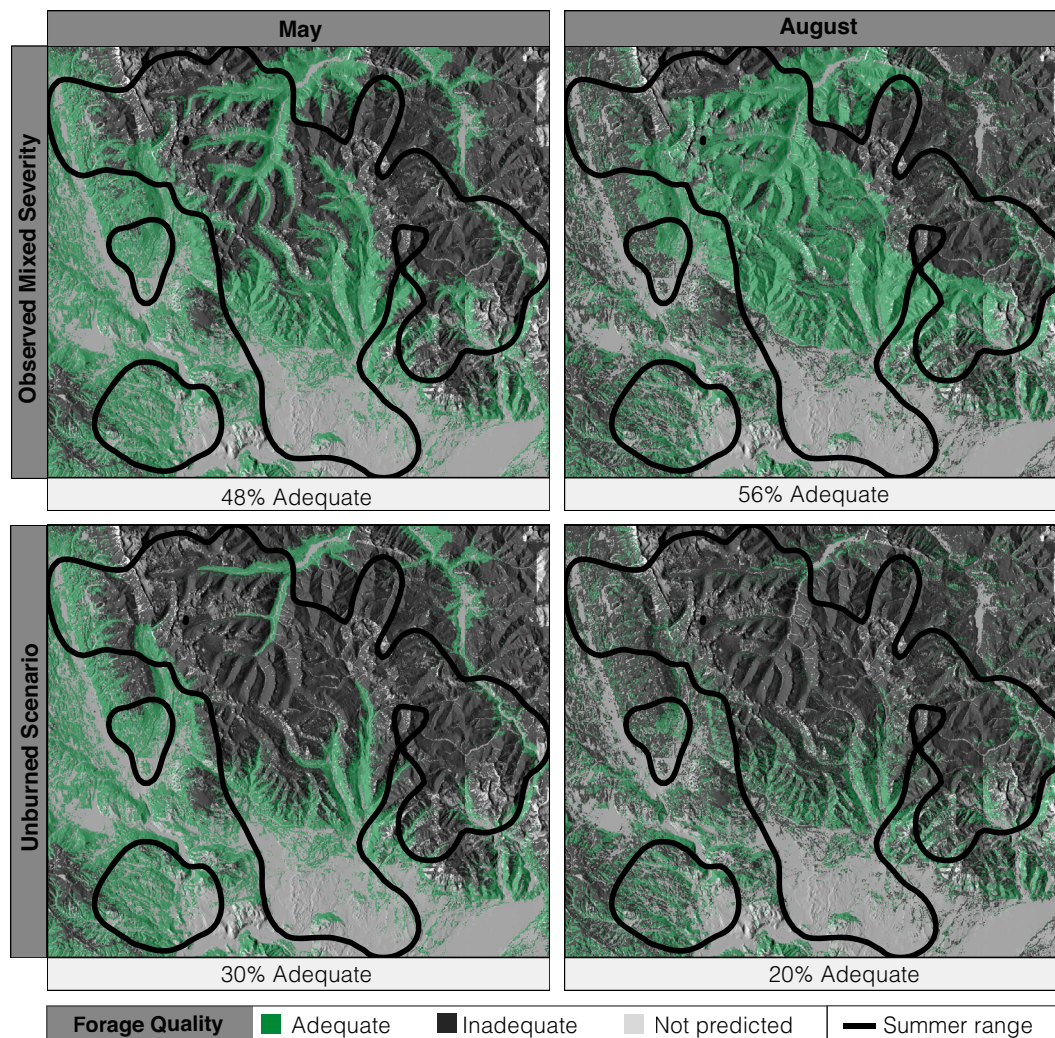
FIGURE 7 Digestible energy predicted onto the observed mixed-severity landscape and the unburned landscape scenario for May and August for the Blackfoot–Clearwater elk population summer range in west-central Montana using the top forage quality model. The percentage of the landscape that meets adequate forage quality (digestible energy > 2.75 kcal/g) increased from May to August for the predicted observed mixed-severity landscape, but the percentage of the landscape with adequate forage quality decreased in an unburned predicted landscape.

the high ratio of highly palatable herbaceous forage to less palatable shrubs within both low- and high-severity burned forests compared with unburned forest (Cook et al., 1994; Merrill et al., 1980; Sachro et al., 2005). Within fire severity classes, low-severity burns tended to have higher forage quality than high-severity burns, but they did not differ significantly. This result is likely due to the overall high proportion of low- and high-severity burned vegetation sampling sites that contained fireweed, an important forage species that rapidly establishes and spreads postfire due to its airborne seeds and rhizomatic nature. Thus, our results predict that fire overall improved forage quality regardless of fire severity. The observed trend of higher forage quality in herbaceous forage compared with shrub forage in this study may differ in other areas across the western United States (Cook et al., 2016).

Differences in forage quality based on lifeform are likely due to variation in plant species found within elk diets and study areas as well as site-level differences.

We found that fire severity variably impacted forage quantity dependent upon forest and forage type. Our results supported our hypothesis that herbaceous forage biomass would be greater in burned compared with unburned forests, but we did not find evidence that there was a significant difference in herbaceous forage biomass between low- and high-severity burns. Herbaceous forage biomass was likely greater in burned forests due to the removal of woody vegetation in the understory and opening of the canopy. The lack of significant difference in herbaceous forage biomass between low- and high-severity burns was likely due to the high proportion of vegetation sampling sites that contained fireweed.

Our results supported our hypothesis that in Years 2 and 3 after the wildfire, shrub forage biomass would be greater in unburned forests, and we found evidence to support our hypothesis that shrub forage biomass would differ based on fire severity. For mesic but not dry forests, shrub forage biomass was significantly greater in areas burned at low-severity compared with high-severity. Fire shifts plant communities to early successional stages, and postfire vegetation regeneration is linked to fire severity (Hollingsworth et al., 2013; Turner et al., 1997, 1999). Fire severity drives postfire plant communities by variably impacting plant survival via the extent of damage to pre-established vegetation (Roberts, 2004). Additionally, fire severity influences recruitment of new individuals by affecting propagule availability and site-specific conditions that influence germination and establishment (Roberts, 2004; Stickney, 1990). Shortly after a wildfire, shrub growth in high-severity burns is limited to new sprouts, whereas in low-severity burns, shrubs also resprout from surviving individuals, a possible explanation for differences in shrub forage biomass between low- and high-severity burns in mesic forests (Roberts, 2004). However, herbaceous forage makes up a larger proportion of the elk population's summer diet; therefore, areas with greater shrub forage biomass may not incentivize elk occupancy as compared to other areas with greater herbaceous forage biomass (Proffitt et al., 2019).

At the landscape-level scale, we found that a large-scale wildfire improved the amount and duration of nutritional resources available to elk throughout the summer shortly after a fire. The unburned landscape scenario predicted the lowest overall percentage of the summer range with adequate forage quality, which declined throughout the summer. The three burned landscape scenarios (completely burned at low or high severity, and the observed mixed-severity fire regime) had a higher predicted percentage of the summer range with adequate forage quality, and an increase in the availability of adequate forage quality throughout the summer. We propose two possible mechanisms to explain why forage quality was higher and why the availability of adequate forage quality increased throughout the summer in the three predicted burned landscapes. First, high DE in burned areas in the early summer decreased throughout the summer but did not decline to inadequate levels. In combination with this effect, vegetation emerged at higher elevational areas in late summer, which resulted in a net gain of the percentage of the summer range with adequate forage quality. On the contrary, in a completely unburned landscape, the areas with adequate DE in the early summer declined to inadequate levels. The addition of high elevation areas with adequate DE in the late summer was not enough to offset the decline at lower elevations, which led to a net loss in the availability of adequate DE.

A second mechanism to explain this pattern is that in the late summer, vegetation in burned areas was generally at earlier phenological stages. This trend suggests that vegetation continued to emerge in burned forests throughout the summer, providing highly palatable and nutritious young plant tissue. These findings differ from previous research that suggested vegetation in prescribed burned forests would senesce earlier because of the reduction in canopy cover, resulting in lower quality forage in burned forests in the late summer (Long et al., 2008). A possible reason for this variation between studies is that prescribed burn effects on nutritional resources for elk differ from wildfires (Proffitt et al., 2019). Prescribed fires typically have reduced severity and smaller extent and occur at different times of the year compared with large-scale wildfires (Ryan et al., 2013). Generally, prescribed burned forests have intact seedbanks and nearby propagule refuge areas leading to no delay in vegetation emerging. Comparatively, large-scale wildfires burn at a higher fire severity and larger extent (Ryan et al., 2013). Shortly after a wildfire, factors influencing germination such as season of burn (Ooi, 2010), reduced propagule availability (Roberts, 2004; Stickney, 1990; Turner et al., 1997), and changed soil characteristics (Certini, 2005) lead to variable rates and patterns of vegetation emergence. Meanwhile, forage in unburned forests emerges in spring and then transitions to later phenological stages, which are frequently more fibrous and less digestible (Van Soest, 1982).

In contrast to the general phenological patterns in our study, we found that forb forage species were in later phenological stages in burned compared with unburned forests in August. The trend of forbs in burned areas having later phenological stages in August is likely explained by fireweed, which begins to fruit and transition into the mature seed stage. Yet, this pattern still contributes to adequate forage quality in burned forests in August because the average DE of fireweed in the fruiting through mature seed stage is ≥2.75 kcal/g (Proffitt et al., 2016, 2019). Therefore, it is important to consider species- and phenophase-specific DE, species composition, and site-level phenology when associating broad phenological trends to ungulate nutrition (Stewart et al., 2006). Our results suggest that fire extended the availability of high-quality forage through multiple mechanisms into late summer when high-quality forage in unburned forests began to wane.

For elk, the late summer and early fall are typically more nutritionally limited compared with the early summer. Our results suggest that a landscape recently impacted by a large-scale wildfire may not have a nutritionally limited late summer (August), which could have strong implications for the nutritional condition of lactating female elk. The highest energetic demands for female

elk are incurred from late spring to mid-summer when lactation occurs, and when elk look to recoup body fat stores lost during the previous winter (Cook et al., 2004). Cook et al. (2004) found that body fat percentages of lactating females were 50% less than nonlactating females during this period. If nutritional resources are inadequate during the late summer and early fall, reproductive pauses may occur if body fat levels are low, but if there is adequate forage quality during this period, lactating females can regain fat reserves, reach fat levels similar to nonlactating females, and, therefore, reproduce (Cook et al., 2004; Proffitt et al., 2016). Thus, the extended availability of high-quality forage into late summer in a burned landscape could positively impact female elk body condition and pregnancy rates.

Although we found that wildfire improved nutritional resource availability in our study area, acquisition of nutritional resources may vary based on a function of risk (DeVoe et al., 2019; Hebblewhite et al., 2009; Middleton et al., 2013). Elk require variable habitats for foraging and security cover, and requirements are inherently tied back to pressures and stressors that exist on a seasonal basis. Wildfires alter the structural characteristics and distribution of these required habitats, which could lead elk to alter their use, and therefore distributions, across the landscape (Pulliam, 2000). For example, recently after a fire, high-severity burned forests were found to have high forage quality in our study area, but the removal of vertical vegetative structure could lead to increased horizontal visibility. Thus, elk vulnerability to predation and human harvest may be higher in high-severity burned forests dependent upon predation strategy and season (Greene et al., 2012). In response, elk may alter their behavior and avoid high-risk areas (DeVoe et al., 2019; Hebblewhite & Merrill, 2009; Spitz et al., 2018). Therefore, changes in the dispersion and availability of both nutritional and security resources are likely to impact elk distributions and acquisition of nutritional resources dependent upon perceived risk.

Large-scale wildfires are becoming increasingly common, and future research is needed to inform wildlife management decisions in the face of disturbances. Our results showed limited differences in nutritional resources between low- and high-severity burned forests shortly after a wildfire. However, burned areas will likely move through successional stages at varying paces, potentially causing more stark differences in nutritional resources between fire severity categories at a later point in time (Turner et al., 1999). Additionally, site-specific variation and climate change will potentially influence the effects of fire severity on forage quality and quantity for elk. For example, high-severity burned dry forests that experience sustained hot and dry conditions postfire could see forests transitioning to grasslands or shrublands (Donato et al., 2016; Stevens-Rumann et al., 2018). Further research is needed to understand the effects of fire severity on forage quality and quantity for elk at varying time steps post-disturbance and in areas with different climatic conditions.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Snobl et al., 2022) are available from Dryad: https://doi.org/10.5061/dryad.b5mkkwhg4.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.