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# Ecological Indicators

Original Articles

# Measures of browse damage and indexes of ungulate abundance to quantify their impacts on aspen forest regeneration

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A B S T R A C T

Ungulate communities are changing at a global scale, which is increasing the need for landscape scale quantification of ungulate impacts on plant communities. To achieve robust monitoring across variable landscapes, managers need quick and reliable indicators for assessing ungulate impacts. Our goal was to evaluate two direct (meristem removal, defoliation) and two indirect methods (fecal counts, camera counts) for evaluating ungulate activity on forest regeneration after fire. We examined the relationships between measures of browse activity (meristem removal, defoliation) of aspen with ungulate community estimates (fecal and camera counts) as a function of variation in physiographic conditions across the study sites. Measurements were made in belt transects at 28 sites across three fires that burned in National Forests in Utah in 2012. Aspen height was best predicted by a model with meristem removal, terrain ruggedness, aspect, and year. Mean aspen height was 5 cm lower for every 10% increase in meristem removal an effect that increased over time. We found moderate correlation between the year and percent defoliation interaction and aspen density. Percent defoliation was related to reduced aspen density in the 2nd and 3rd years but not in the 1st year. Results demonstrated that meristem removal is correlated closely with ocular estimates of defoliation ($r^2 = 0.83$), ungulate abundance using fecal counts ($r^2 = 0.65$) and camera counts ($r^2 = 0.63$). Fecal counts and camera counts also correlated well with each other ($r^2 = 0.74$). Estimates of meristem removal in our study suggest that 75% browse of apical meristems is an important threshold for successful aspen height growth and 50% defoliation for aspen regeneration density. Our study highlights the strengths of measurements of meristem removal and defoliation to predict ungulate effects on forest recruitment potential.

## 1. Introduction

Ungulate herbivory can have strong top-down effects on the abundance and composition of plant communities (Augustine and McNaughton, 1998; Carpio et al., 2015; Hobbs, 1996; Waller and Alverson, 1997). Ungulate communities and populations are changing drastically due to management of ungulate populations and introduction of non-native ungulates (Spear and Chown, 2009; Waller and Alverson, 1997). There is strong evidence that growing ungulate populations limits the regeneration of palatable tree species and reduces plant diversity (Augustine and Frelich, 1998; Edenius et al., 2011; Kaufmann et al., 2014; Rooney and Waller, 2003). As a result, there is increased interest in understanding how changing ungulate herbivory regimes are affecting forest recruitment at landscape scales (Frerker et al. 2013). However, accurate characterization of ungulate impacts on vegetation at large spatial scales is technically challenging due to the large degree of variation and complexity across landscapes (Frerker et al., 2013; Waller et al., 2009). Therefore, development and

comparison of indexes characterizing ungulate impact on ecologically important species is increasingly important under changing herbivory regimes.

Ungulate impacts on ecologically important pioneer plant species are well studied, yet often show conflicting patterns (Bartos et al., 1994; Barnett and Stohlgren, 2001; Kauffmann et al., 2010; Randall and Walters, 2011; Ripple et al., 2001). Differences in the methodologies used could contribute to the inconsistency in observed results (Waller et al., 2009). Studies that quantify the impact of ungulates on plant communities generally use two methodological approaches. The first method estimates ungulate population size to infer relative effect on plants across different study areas (Rooney and Waller, 2003; Waller et al., 2009). We refer to this first approach as "indirect" because it assumes that the number of ungulates is proportional to their impact on one or more plant species (Morellet et al., 2001). The second approach is to evaluate the ungulate herbivore damage on the focal plant by some measure of damage to plant tissue. We refer to this approach as "direct" given that the focal plant species is used directly to evaluate ungulate

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impact. Selecting optimal methods for estimating ungulate impacts on plant communities is crucial for effective management, yet few studies have explicitly compared the efficacy of multiple methods (Waller et al., 2009).

Indirect methods have been the basis of evaluating ungulate impacts for decades and generally estimate relative abundance through fecal counts, camera counts, or management derived population estimates (Barnett and Stohlgren, 2001; Randall and Walters, 2011; Rooney and Waller, 2003; Seager et al., 2013). Indirect methods have proven useful when compared to other estimates of ungulate habitat use (Loft and Kie, 1988), and can inform management decisions (Barnett and Stohlgren, 2001; Wan et al., 2014). Fecal counts have been successfully used since the 1940′s to estimate relative abundance of ungulates (Bennett et al., 1940) and are often combined with assumptions about defecation rates to extrapolate population size (Neff, 1968; Royo et al., 2016). In recent years, camera-traps have been used for estimating animal abundance (Clare et al., 2015; Long et al., 2007), and ungulate behavior and forage patterns in plant communities (Faison et al., 2016a). Use of management derived population estimates have been used to estimate ungulate impact on plants (Seager et al., 2013). However, due to the wide variety of methods (Loft and Kie, 1988) and the known inaccuracies in estimating population sizes (Krebs, 1999; Waller et al., 2009) these methods may prove less useful at landscape scales (Frerker et al., 2013).

Indirect methods of quantifying ungulate impacts on vegetation have the advantage of identifying consumers when multiple herbivores are present (Rhodes et al. 2017a,b) but they generally have low model fit and predictability (Rhodes et al. 2017a; Rooney and Waller 2003; Stewart et al. 2009). This is likely due to confounding effects such as: changing forage availability, topography and climate across sites (Frerker et al. 2013; Rhodes et al. 2017a). Linking estimates of ungulate abundance directly to their impact on the plant community is challenging due to the high mobility of ungulates and inaccurate methods of estimating mobile animal populations (Krebs, 1999; Waller et al., 2009). For these reasons, there is increasing interest in using direct methods to assess ungulate impacts on focal plant species (Frerker et al., 2013).

Quantifying direct ungulate impacts on plants by measuring browse damage, accurately measures the impact but identifying the ungulate species responsible can be challenging (Frelich and Lorimer 1985; Rooney and Waller 2003; Waller et al. 2009). Direct measurements of ungulate impact on plants include removal of meristems (McInnes et al. 1992; Wan et al. 2014), removal of leaf tissue or indices that use a single plant species as indicators of ungulate impact (Balgooyen and Waller 1995; Frelich and Lorimer 1985; Mason et al. 2010; Rooney and Waller 2003). Ocular estimations of removal of leaf tissue could be analogous to percent cover. Ocular cover estimates, while often considered highly subjective, can be similar to and more efficient than more complex methodologies (Vales and Bunnell 1988). Direct methods sometimes allow differentiation between vastly different herbivores (hares vs. moose, McInnes et al. 1992), but distinguishing between ungulates can be difficult (Faison et al. 2016b).

Aspen (*Populus tremuloides* Michx.) forests are model systems for understanding plant-herbivore interactions because they provide habitat and forage for many herbivore species and their defense chemistry is well characterized (Lindroth and St. Clair, 2013). There is concern that heavy browsing of aspen by ungulate in some areas may contribute to aspen decline (Lindroth and St. Clair, 2013; Seager et al., 2013). In the Intermountain West, fire is a major driver of aspen regeneration and retention across the landscape (Romme et al., 2005; Smith et al., 2011a). Aspen is particularly susceptible to ungulate herbivory as root suckering occurs after fire (Seager et al., 2013). However, there is considerable controversy over the magnitude of the impact of ungulates on aspen recruitment (Kauffmann et al., 2010; Rhodes et al., 2017a; Ripple et al., 2001; Romme et al., 2005). Vertical escape through height growth is an important aspen defense strategy against ungulate herbivory, and sufficient density is needed for stand replacement after fire

(Bartos et al., 1994; Rhodes et al., 2017b; Seager et al., 2013). Monitoring of aspen regeneration has shown acute failure of aspen regeneration after fire in some areas (Bartos et al., 1994; Ripple et al., 2001) and stable regeneration despite high ungulate densities in other locations (Barnett and Stohlgren, 2001; Romme et al., 2005). Aspen regeneration success can vary depending on climate, topography and stand composition (Rhodes et al., 2017a; Smith et al., 2011a), which can confound our understanding of the direct effect that ungulates have on aspen regeneration success. Further, quantifying ungulate impacts on plants is inherently complex given the diversity and complexity of ungulate behavior and diet (Beck and Peek, 2005; Long et al., 2014).

Exploring the advantages and disadvantages of various methods for quantifying ungulate impacts on aspen regeneration and recruitment is vital to managing for resilience and sustainability of forest ecosystems. Our central research question was: which measures of ungulate impact are best for predicting aspen establishment and recruitment in post-fire environments across large landscapes? The objective of this study was to compare the efficacy of common methods for estimating ungulate impact on aspen. We measured the height and density of aspen regeneration for three years post-fire. We then compared the relative performance of four methodologies (two indirect and two direct) for estimating ungulate impact on aspen regeneration. Secondly, we used physiographic features to account for variation in the impact of ungulate species on aspen regeneration due to topography. We predicted that aspect, terrain ruggedness, and elevation would influence aspen vertical growth and density. We hypothesized that aspen height would be better estimated by direct methods given that loss of plant tissue can translate into reduction of height. Finally, we predicted that aspen density would be better estimated by indirect methods of estimating ungulate impact because removal or death of aspen through herbivory is likely related to total ungulate number.

## 2. Materials and methods

### 2.1. Study area

This study was conducted in post-fire environments in mixed aspen-conifer forests across three National Forests of central and southern Utah. Our study consisted of 28 sites across three fires that burned in summer 2012 that demonstrated aspen suckering in the fall of 2012 (Fig. 1). Fire sizes ranged from 900 to 19,400 hectares. Site elevations ranged from 2500–3030 m and slope ranged from 1 to 28 degrees. Thirty year mean annual precipitation ranged from 380 to 800 mm. Dominant tree species in the Seeley and Box Creek fires included: Aspen, Subalpine Fir (*Abies lasiocarpa* (Hooker) Nuttall) and White Fir (*Abies concolor* (Gordon) Lindley ex Hildebrand). While the dominant conifer component of Harris Flat fire is Ponderosa Pine (*Pinus ponderosa* Douglas ex C. Lawson). Cattle (*Bos taurus*), Mule deer (*Odocoileus hemionus*), and American elk (*Cervus canandensis*) were the most abundant ungulates herbivores at the study sites.

### 2.2. Sampling design

Eight sites were established in 2012 and the remaining 20 were established in May 2013. At each site we established one 50 × 2 meter belt transect for characterizing aspen regeneration density, height, damage to aspen and fecal counts. The first samples were taken in September 2013. In total, there were 15 sites in the Seeley fire, 8 sites at the Box Creek fire, and 5 sites at the Harris Flat fire. We randomly selected the direction of each belt transect and marked both end points with u-posts and GPS waypoints. In September of 2013, 2014, and 2015 we surveyed aspen sucker regeneration responses and herbivory patterns along these transect lines. We defined an aspen sucker as emerging independently from the ground (unbranched above ground level) within transects.
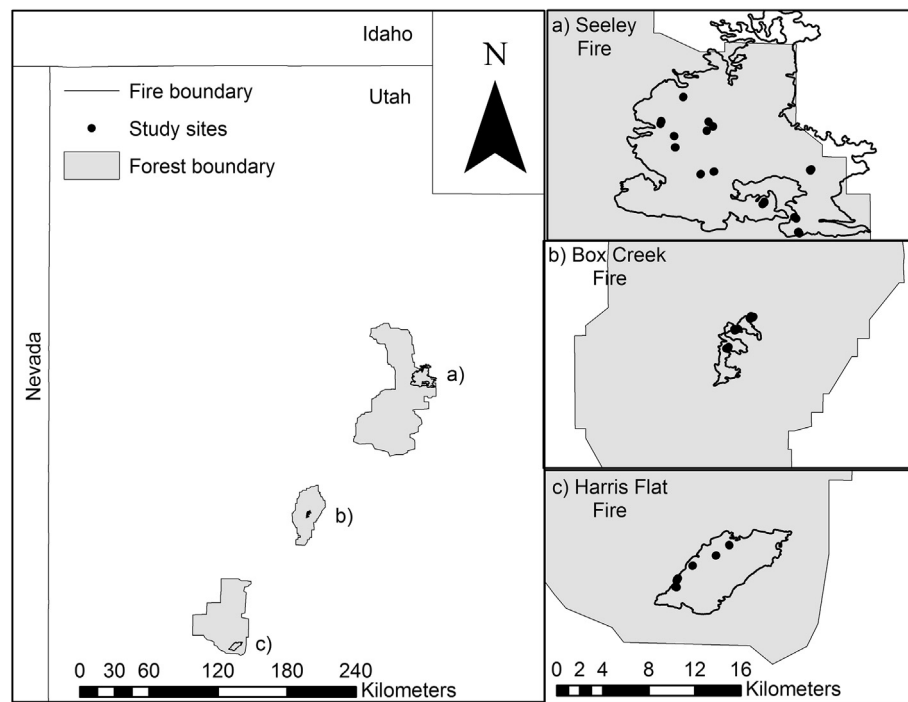
**Fig. 1.** A map of the study area depicted on a small-scale map (1:5,000,000) with partial national forests and fire perimeters. Fires are labeled a, b, and c (Seeley, Box Creek, and Harris Flat, respectively). Inset maps are displayed to the right in a larger scale of 1:500,000. Solid black points mark the study sites in the three inset maps.

## 2.3. Direct methods

### 2.3.1. Apical meristem removal (%)

Meristem removal was characterized by examining the percent of apical meristems removed by herbivory from the leading branch and the sub-leading branches in the top 15 cm of an aspen sucker (Jones et al., 2005; Rhodes et al., 2017a; Wan et al., 2014). Aspen suckers with multiple sub-leaders were quite common, and the entire stem was considered browsed if all meristems were removed. Aspen were considered suckers and sampled if they were 1–200 cm in height, and within the reach of ungulates (Rhodes et al., 2017a). Site-specific percent browse is reported as the number of browsed stems within each transect versus stems that have apical meristems intact. Meristems were characterized as intact, browsed, or other (damage from frost, pathogen infection, and drought).

### 2.3.2. Ocular estimates of defoliation (%)

We treated ocular estimates of defoliation as analogous to ocular estimates of cover. We recorded percent defoliation as observed foliar tissue divided by estimates of potential leaf cover in the absence of herbivory. Ocular estimates of defoliation of aspen were taken from aspen within the 50 m × 2 m belt transects by walking the line and observing leaf cover removal of aspen within the transect. Estimates were given for the total transect and rounded to nearest 5% in order to increase speed of observations and reduce potential site-to-site, or year-over-year bias. Observations were made by a single observer for the duration of the study to eliminate observer bias. While ocular estimates of cover have the disadvantage of being subjective, training in ocular techniques can standardize estimates (Vales and Bunnell, 1988). Ocular estimates of cover can lead to similar results as more time-consuming estimates that use complex grids or assessment of multiple subplots (Vales and Bunnell, 1988).

## 2.4. Indirect methods

### 2.4.1. Fecal counts

In each transect, we surveyed fecal counts of American elk (*Cervus*

*canandensis*), mule deer (*Odocoileus hemionus*), and cattle (*Bos taurus*) (Neff, 1968). We used the following criteria for counting first year fecal counts: 1) we excluded any feces that were under leaf litter, as this is an indication that they were deposited before the previous fall. 2) Any feces that presented a whitish color, indicative of advanced stages of decay was excluded. 3) Feces were cleared from the plots after being surveyed. A pellet group was considered a count when 3 or more pellets were clustered and from the same defecation event based on size and color (Neff, 1968). Mule deer, American elk and cattle fecal matter were easily distinguishable by their size and shape (Rost and Bailey, 1979). Average fecal counts in transects were 16.4 ± 2.1 and ranged from 0 to 57.

### 2.4.2. Camera counts

At the end of each transect we placed a trail camera (PC900 HyperFire Professional Covert Camera Trap) (Reconyx, Holmen, WI, USA) to estimate an index of relative use by ungulate species (O'Brien et al., 2011). We used ungulate counts per camera per day (ungulate camera$^{-1}$ day$^{-1}$) as an estimate of ungulate presence at each site. Cameras were at one end of each transect facing down the transect line. Cameras were set at medium sensitivity to capture five photos at three-second intervals with a five-minute rest period in between triggers. Each ungulate that appeared at least once in the five-photo set were counted and these counts were summed and divided by the number of active camera days for each plot. Average ungulates per camera day were 1.03 ± 0.17 and ranged from 0 to 5.7 over a total of 4319 camera days.

## 2.5. Topographical features

We considered elevation, aspect, and terrain ruggedness to be important topographic features influencing aspen height and density (Rhodes et al., 2017a). We extracted elevation from a 30 m × 30 m digital elevation model (DEM) of Utah and associated it with the GPS coordinates of our sites. We extracted aspect from the DEM, converted the angles into radians and took the cosine in order to get a "northness" value, where 1 = North, and −1 = South. We used the standard

**Table 1**

*A priori* model results with topography as a predictor of aspen height. The associated model parameters (K), change in AICc when compared to the top model and the Akaike weights are listed for each model.

| Aspen Height Topographical Models | K | ΔAICc | Weight (%) |
|---|---|---|---|
| Intercept only | 2 | 53 | < 0.01 |
| Year + Site | 5 | 4 | 9 |
| Terrain Ruggedness + Year + Site | 6 | 8 | 1 |
| Elevation (m.a.s.l.) + Year + Site | 6 | 5 | 5 |
| Northness + Year + Site | 6 | 7 | 2 |
| T. Ruggedness + Elevation + Year + Site | 7 | 8 | 1 |
| Elevation + Northness + Year + Site | 7 | 5 | 6 |
| *T. Ruggedness + Northness + Year + Site | 7 | 0 | 63 |
| T. Ruggedness + Elevation + Northness + Year + Site | 8 | 3 | 14 |

deviation of slope in a 3 × 3 neighborhood of cells surrounding the pixel of our site to calculate terrain ruggedness (Grohmann et al., 2011). We chose this index because of its simplicity, and ability to distinguish ruggedness at local and regional scales and its robustness across changes in resolution (Grohmann et al., 2011). All extractions of topographical features were completed in ArcMap (ESRI 2016).

## 2.6. Statistical analysis

We used model selection to determine relative model support for aspen height and density (analyzed separately) using linear regression and variance weighted across years due to heterogeneity of variance. We judged relative model support using Akaike's Information Criterion (AICc) (Akaike, 1973; Burnham and Anderson, 1998). First, we compared relative support for preliminary models that included all combinations of topographical features elevation, northness, and terrain ruggedness and with year and site against intercept only models for aspen height and aspen density, separately (Tables 1 and 2). After finding an optimal preliminary model, we used model selection to determine relative support for the four methods (direct: meristem removal and defoliation; indirect: camera counts and fecal counts) of estimating ungulate impact on aspen regeneration after fire. We further broke down total camera and fecal counts by species and compared those models with the rest of the four methods. We then compared the four methods for estimating ungulate effect on the aspen height and density against the best topographic model, and the intercept only model respectively (Tables 3 and 4). In our case, we could not distinguish between ungulate species type by direct measures, and both the indirect measures (fecal and camera counts) showed multicollinearity with fire, making separation of ungulate species problematic. Further, the models that differentiated between ungulate species were less parsimonious than the summed models (Tables 3 and 4). Therefore, we binned all species together for both fecal and camera counts.

As a complement to our model selection, we also compared goodness-of-fit for each model (r²) (Table 5). Finally, we used linear regression to model each of the four direct and indirect indicators against

**Table 2**

*A priori* model results with topography as a predictor of aspen density. The associated model parameters (K), change in AICc when compared to the top model and the Akaike weights are listed for each model.

| Aspen Density Topographical Models | K | ΔAICc | Weight (%) |
|---|---|---|---|
| Intercept only | 2 | 18 | < 0.01 |
| Year + Site | 6 | 10 | < 0.01 |
| Terrain Ruggedness + Year + Site | 7 | 7 | 2 |
| Elevation (m.a.s.l.) + Year + Site | 7 | 12 | < 0.01 |
| *Northness + Year + Site | 7 | 0 | 75 |
| T. Ruggedness + Elevation + Year + Site | 8 | 15 | < 0.01 |
| Elevation + Northness + Year + Site | 8 | 13 | < 0.01 |
| T. Ruggedness + Northness + Year + Site | 8 | 3 | 22 |
| T. Ruggedness + Elevation + Northness + Year + Site | 9 | 15 | < 0.01 |

**Table 3**

*A priori* model results with each of the four methods of estimating ungulate impact as a predictor of aspen height. The associated model parameters (K), change in AICc when compared to the top model and the Akaike weights are listed for each model.

| Aspen Height Methodology Models | K | ΔAICc | Weight (%) |
|---|---|---|---|
| Intercept only | 2 | 130 | < 0.01 |
| Topographic Model (TM) + Year + Site | 7 | 65 | < 0.01 |
| TM + Meristem % removal × Year + Site | 11 | 0 | < 0.01 |
| TM + Defoliation × Year + Site | 11 | 15 | < 0.01 |
| TM + Camera Counts* × Year + Site | 11 | 67 | 92 |
| TM + Camera Counts (cattle, elk, deer) + Year + Site | 11 | 59 | < 0.01 |
| TM + Fecal Counts × Year + Site | 11 | 16 | < 0.01 |
| TM + Fecal Counts (cattle, elk, deer) + Year + Site | 11 | 5 | 7 |

**Table 4**

*A priori* model results with each of the four methods of estimating ungulate impact as a predictor of aspen height. The associated model parameters (K), change in AICc when compared to the top model and the Akaike weights are listed for each model.

| Aspen Density Methodology Models | K | ΔAICc | Weight (%) |
|---|---|---|---|
| Intercept only | 2 | 27 | < 0.01 |
| Topographic Model (TM) + Year + Site | 6 | 16 | < 0.01 |
| TM + Meristem % removal × Year + Site | 10 | 9 | 1 |
| TM + Defoliation* × Year + Site | 10 | 0 | 98 |
| TM + Camera Counts × Year + Site | 10 | 10 | < 0.01 |
| TM + Camera Counts (cattle, elk, deer) + Year + Site | 10 | 11 | < 0.01 |
| TM + Fecal Counts × Year + Site | 10 | 16 | < 0.01 |
| TM + Fecal Counts (cattle, elk, deer) + Year + Site | 10 | 15 | < 0.01 |

**Table 5**

Full model goodness of fit are presented for each indicator for both height and density. Below both total camera and total fecal count models are presented models that differentiate between species for each methodology.

| Model | Index | r² |
|---|---|---|
| *Aspen Height* | Meristem % rem. | 0.90 |
| | Defoliation % | 0.86 |
| | Camera Counts | 0.63 |
| | Cattle, Deer, Elk | 0.58 |
| | Fecal Counts | 0.61 |
| | Cattle, Deer, Elk | 0.59 |
| *Aspen Density* | Meristem % rem. | 0.40 |
| | Defoliation % | 0.44 |
| | Camera Counts | 0.27 |
| | Cattle, Deer, Elk | 0.23 |
| | Fecal Counts | 0.28 |
| | Cattle, Deer, Elk | 0.11 |

each other in paired combinations (e.g. removal of apical meristem % vs. defoliation %, or camera counts vs. fecal counts). For this we used a linear regression and paired each indicator as a response variable in combination with all other indicators as explanatory variables. We also included year and site as a fixed effect. We had a total of 6-paired combinations and assessed their correlation using the full model. To verify assumptions of normality and homoscedasticity in the error structure for the top model, we visually inspected residual plots. Density counts were square root transformed to meet the assumption of normality, and in order to use AIC for comparison between aspen density models (Zuur et al., 2009). We used the MuMIn (Barton, 2015) package of Program R (R Core Team, 2015) for all analyses.

## 3. Results

### 3.1. Preliminary topographical models

Topography appeared in the most parsimonious model for both aspen height and density in the preliminary models. The topography model including both terrain ruggedness and northness had 63% of the

Akaike weight and was significantly better than the intercept only model for aspen height (Table 1). The goodness of fit for the top topographical model for height was $r^2 = 0.60$. Terrain ruggedness was positively correlated with aspen height (3.5 cm $\pm$ 1.3 cm). The parameter estimate for northness included 0 in its error range and therefore was a poor predictor of height despite being in the top model. Therefore, it was removed from the final model.

Including northness in the model was an improvement over the intercept only model for aspen density, with 75% of the Akaike weight (Table 2). The goodness of fit for the top topographical model for density was $r^2 = 0.26$. The two closest models including terrain ruggedness, or terrain ruggedness and northness had greater than 2 ΔAIC and were, therefore, not included in the subsequent model. The northness parameter estimate included 0 in its error range. Therefore, despite being the most parsimonious model through our AICc methodology, it was a poor predictor of aspen regeneration density. Therefore, it was removed from the final model.
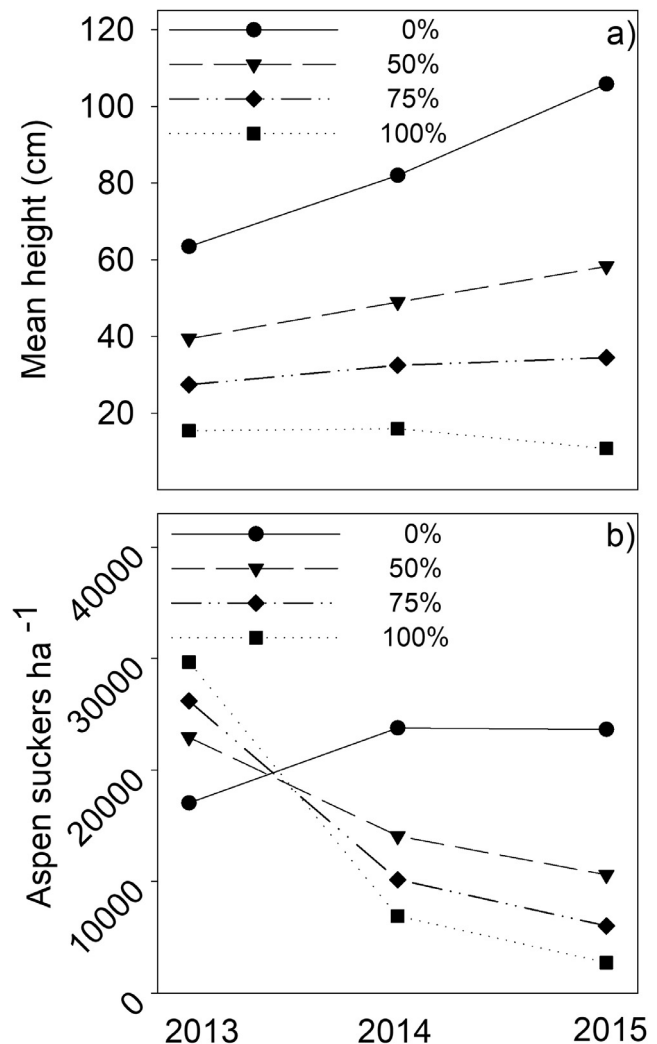
### 3.2. Top models for aspen height and density

The results of model selection indicated that meristem removal was clearly the top model with 92% of the AIC weight (Table 3). The percent of apical meristems removed showed a strong relationship with sucker height. For each 10% increment in apical meristem removal, the model predicted 5 $\pm$ 2.4 cm reduction in height (Table 6). When adjusted for yearly growth patterns, our model indicated that height growth was suppressed at ≈75% apical meristem removal (Fig. 2). The maximum and minimum mean heights recorded after three years of growth was 130 and 11 cm respectively and the mean height $\pm$ 1 SE at years 1, 2 and 3 were 37 $\pm$ 4, 53 $\pm$ 5, and 66 $\pm$ 7 cm, respectively.

Maximum and minimum aspen density across sites at the beginning of the study was 35,000 and 5,000 suckers/ha. By the end of our study the maximum and minimum were 44,000 and 500 suckers/ha, respectively. Average aspen density was 17,000/ha across the study period. Our top model for predicting aspen density included defoliation (%) with 92% of the AIC weight (Table 4). Neither percent defoliation nor year were significant predictors of density but their interaction was (Table 6). Specifically, defoliation had a slightly positive but statistically insignificant effect on aspen density the first year after fire, but began to reduce aspen density in the 2nd and 3rd year of the study (Fig. 2c).

### Table 6

Beta estimates for the top models previously selected are presented along with their associated standard error and t-statistic. Aspen height units are centimeters, and aspen density units are the number of suckers 100 m$^{-1}$. We list the estimate, the standard error associated with it and the t-statistic.

| Aspen Metric | Parameter | Estimate | SE | t |
|---|---|---|---|---|
| *Aspen Height* | Intercept | 61 | 15 | 3.9 |
| | Meristem % rem. | −0.5 | 0.2 | −2 |
| | Year 2014 | 16 | 16 | 0.9 |
| | Year 2015 | 38 | 16 | 2.4 |
| | Northness | −5 | 3.3 | −1.5 |
| | Harris Flat | 8.7 | 5.2 | 1.6 |
| | Seeley | 5.1 | 5.0 | 1.0 |
| | Meristem % rem:2014 | −0.1 | 0.3 | −0.5 |
| | Meristem % rem:2015 | −0.4 | 0.3 | −1.6 |
| *Aspen Density* | Intercept | 12 | 2.9 | 4.0 |
| | Defoliation % | 0.04 | 0.05 | 0.8 |
| | Year 2014 | 2.4 | 2.5 | 1.0 |
| | Year 2015 | 2.4 | 2.5 | 1.0 |
| | Harris Flat | 2.1 | 2.2 | 1.0 |
| | Seeley | 1.4 | 2.1 | 0.7 |
| | Defol %:2014 | −0.1 | 0.05 | −2.3 |
| | Defol %:2015 | −0.2 | 0.05 | −2.9 |



**Fig. 2.** Predicted mean height of aspen or mean aspen density is shown across the study period, using the top model from Table 6. For aspen height we account for aspect by holding northness at 0 (east or west aspect). Change in aspen height is presented as a function of percent removal of apical meristems and its interaction with year is presented in panel (a), while the effect of percent defoliation on aspen density and its interaction with year is presented in panels (b).

### 3.3. Comparison of methodologies

We found that removal of apical meristem and measures of percent defoliation had high goodness of fit for height and moderately good fit for aspen suckering density (Table 5). We found that all four methodologies were significantly correlated, yet the strength of that relationship differed between indirect and direct measures. Mixed modeling showed high correlation between removal of apical meristems and defoliation ($r^2 = 0.83$) and between fecal counts and camera counts ($r^2 = 0.74$). Correlation between removal of apical meristems and both fecal counts and camera counts were more modest ($r^2 = 0.55$, $r^2 = 0.56$). Correlation was moderate between defoliation and both fecal counts and camera counts ($r^2 = 0.63$, $r^2 = 0.65$). In summary, correlation within direct and indirect methodologies was high and statistically significant, with correlation coefficients between methodologies tending to be lower (Fig. 3).
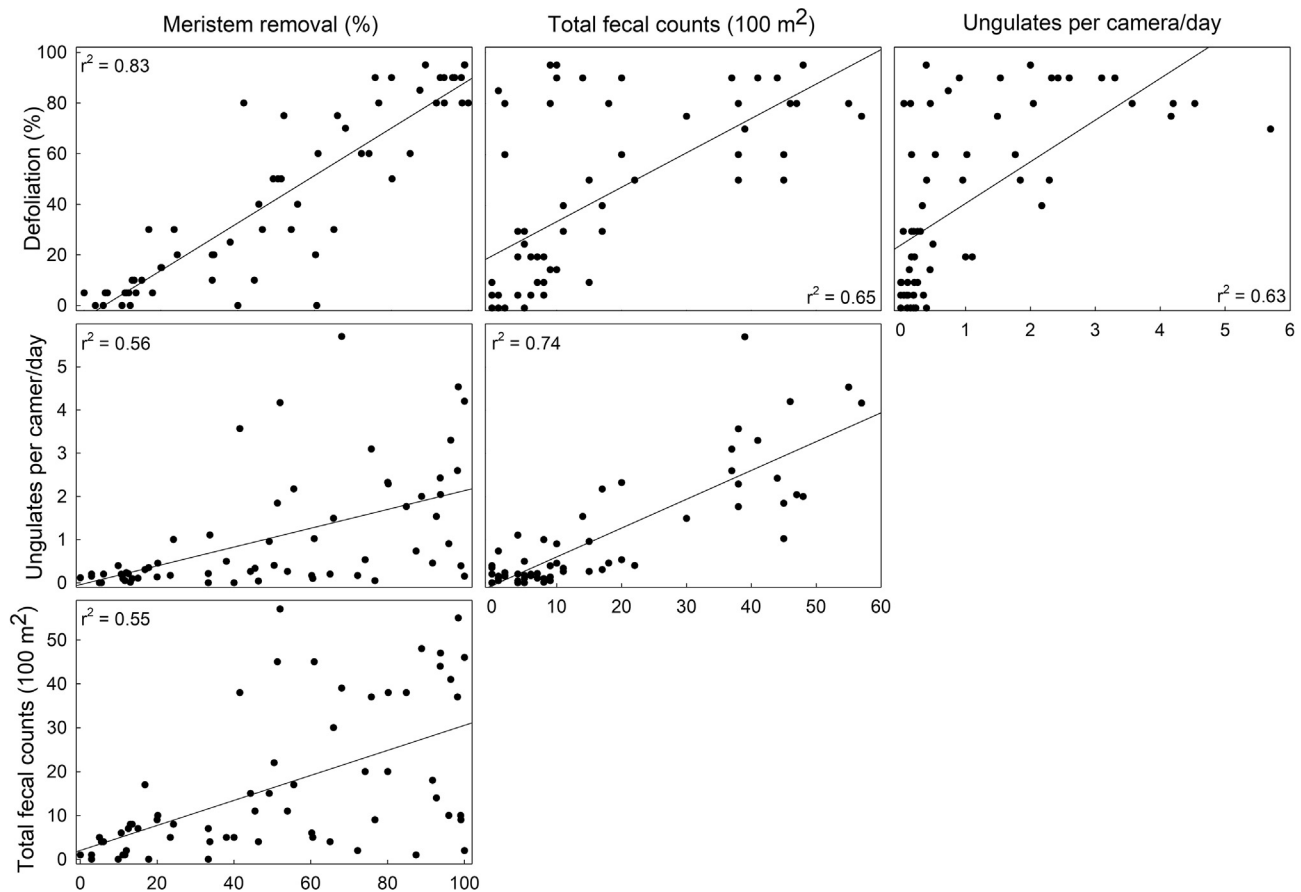
**Fig. 3.** Pairwise regression analyses are presented here which the relationships between meristem removal (%), defoliation (%), ungulate camera counts/day and fecal counts/100 m. The $r^2$ values represent the full model including year, fire location, northness, and terrain ruggedness. The points represent raw values.

## 4. Discussion

### 4.1. Indicators of height and density

Despite aspen's fast growth rates in post burn environments (Wan et al., 2014), aspen regeneration and recruitment success can be reduced by ungulate herbivory (Bartos et al., 1994). Ungulates suppress aspen forest recruitment after fire by slowing height growth, and reducing suckering density (Romme et al., 2005; Rhodes et al., 2017a,b). Our results suggest that meristem removal was the best predictor of aspen suckering height (Table 6). Aspen height growth is a key component to defense against ungulates through vertical escape (Lindroth and St. Clair, 2013), and recruitment in the understory is important to long-term aspen stand resilience and health (Kaye et al., 2005; Smith et al., 2011b). These results are consistent with other studies that also found that meristem removal was a useful indicator of ungulate impact on regeneration and recruitment in other forest types (Frerker et al., 2013; Royo et al., 2016).

The interaction between percent defoliation and year suggest that changes in density due to ungulate impact are longer term effects (Fig. 2c). This is likely because pre-fire stand composition has a stronger influence on initial aspen regeneration density (Smith et al., 2011a) and clonal integration of aspen provide resource storage for aspen which increases resilience (Rhodes et al., 2016). Stability in initial tree densities after disturbance is consistent with studies in eastern hardwood forests of the US showing that deer browsing reduces vertical growth of hardwood seedlings but not stand density (Royo et al., 2016). Aspen's clonal growth habit through which connected trees share resources may allow browsed suckers to persist for decades without recruiting into the overstory (Rhodes et al., 2017b). Our results indicate that at least three

years of monitoring aspen density after fire is necessary to evaluate ungulate impact on aspen forest replacement.

Topography can influence the regeneration success of aspen (Dudley et al., 2015) by modifying ungulate behavior and altering the physiological function of aspen (Long et al., 2014; Rhodes et al., 2017a). Topographical conditions that provide better light or water availability increase aspen resilience to ungulate herbivory (Wan et al., 2014; Rhodes et al., 2017a). Similar to our study, high physiological function on southern aspects contributed to taller and better defended aspen on southern facing slopes (Wan et al., 2014). The high energetic cost of ungulate movement over rugged terrain can reduce habitat selection and vegetation use in these areas (Long et al., 2014). We found that terrain ruggedness increased height of aspen regeneration which suggests that ungulate reduction of aspen height was hindered at rugged sites (Table 6). While elevation is generally correlated with higher aspen regeneration and recruitment (Rhodes et al., 2017a) the limited range in elevation (2500–3030 m) in our study likely resulted in little influence of elevation in our study. While only terrain ruggedness estimates were significant, both northness and terrain ruggedness contributed to the most parsimonious models as evidenced by AICc model selection. Our findings support the broader scientific literature suggesting that topographical features should be included when evaluating ungulate impacts on aspen regeneration.

### 4.2. Comparing indicators of ungulate herbivory

We found high correlations within direct and indirect measures of aspen regeneration success with lower but still good correlations between direct and indirect measures (Fig. 3). Ocular measurement of foliar cover are generally considered highly subjective, yet in some

cases can provide similar results to more complex or costly methods (Vales and Bunnell, 1988). Our results suggest that measuring ocular estimates of defoliation was similar to removal of apical meristems, but with much less investment in time. With a single observer, this quick method tended to correlate well with more time intensive measurements of meristem removal (Fig. 3). Further, direct measures can be extended to estimate local abundances of ungulates and alert managers to high ungulate abundances at the local scale (Fig. 3) (Rhodes et al., 2017a; Royo et al., 2016). This method did not differentiate between missing foliage due to insect herbivory and may not be useful in areas with high insect defoliation.

One of the advantages of estimating ungulate populations or indexing their abundance is to identify which ungulate species is responsible for impacting aspen recruitment. In our case, we could not distinguish between ungulate species type by direct measures, and while indirect measures pellet groups and camera counts accurately identified the species we could not distinguish between species due to multicollinearity between fire location and the mix of species that frequented our plots. However, total fecal counts and camera counts showed good correlations with measures of browsing impact (Fig. 3). There is increasing evidence that the abundance of the ungulate community is more important than composition of the ungulate community in assessing impacts on aspen regeneration (Bork et al., 2013; Rhodes et al., 2017a; Walker et al., 2015). The data suggest that direct measures of damage to aspen provide good estimates of relative use by the ungulate community (Fig. 3). This is consistent with work in other forest systems showing good correlations between presence of ungulates and browse impacts (Royo et al., 2016).

### 4.3. Indicator precision, reliability and feasibility

Use of browsing indexes are considered a reliable ecological indicator (Frerker et al., 2013) and often correspond to fecal counts of ungulates (Royo et al., 2016). There is a growing base of literature that supports the reliability of removal of apical meristems as an ecological indicator for ungulate-aspen interactions (Kaye et al., 2005; Strand et al., 2009; Rhodes et al., 2017a; Wan et al., 2014). Our data suggest that removal of apical meristems is precise with a low standard error around our estimate ( ± 0.2 cm, Table 6) which may contribute to its use as a monitoring tool and for defining thresholds for ungulate influence on aspen regeneration dynamics. Removal of apical meristems has been used as a monitoring tool for decades (Olmsted, 1979; Jones et al., 2005) and estimates of thresholds where ungulates begin to influence aspen regeneration are converging at around 30% (Olmsted, 1979; Strand et al., 2009; Rhodes et al., 2017b). Our study found that ocular estimates of defoliation may replace or supplement the more work intensive measurement of removal of apical meristems (Table 5). Ocular estimates of simulated defoliation by insects have been shown to have high precision and accuracy with a reduction in bias with experience (Johnson et al., 2016). However, we suggest more work is necessary to develop the ocular defoliation indicator for aspen in the field. This research may compare, among many possibilities: reliability and accuracy across sites and observers.

Use of fecal counts also has a long history of use as an ecological indicator (Neff, 1968; Seager et al., 2013). However, fecal counts provide results that at times are helpful (Rogers and Mittanck, 2014), but may also offer poor predictive power (Rhodes et al., 2017a,b). Camera traps and pellet counts can achieve high accuracy for estimating ungulate abundance (Marques et al., 2001; Rovero and Marshall, 2009), but neither alone accurately estimates ungulate impact on their habitat (Morellet et al., 2007). Our data suggest that, from a management perspective, estimating ungulate impact through measurements of damage to aspen tissue may be the most precise, reliable, and feasible.

### 4.4. Management implications

Ungulate communities are changing on a global scale (Spear and Chown, 2009) and have the capacity to alter forest regeneration and recruitment (Rooney and Waller, 2003). There is an increasing need to monitor ungulate impacts at landscape scales (Frerker et al., 2013). However, the inherent variation in landscape scale topography and ungulate movement confound our ability to link ungulate impact to forest regeneration. In previous studies, ungulates halted aspen regeneration (Bartos et al., 1994; Kay, 1998). However, these studies were conducted in areas known to have high ungulate populations. In regional studies, aspen regeneration failure due to ungulate herbivory has been shown to be much more variable (Rogers and Mittanck, 2014; Rhodes et al., 2017a). Therefore, extrapolation of ungulate effects on plant species outside of the study or monitoring area should be used with extreme caution, especially when monitoring lacks spatiotemporal breadth and are known to have high ungulate densities (Suzuki et al., 1999).

In the face of this uncertainty, we present data that identifies critical herbivory thresholds for regenerating trees that is broadly applicable. Meristem removal measurements clearly predicted growth potential in post-fire environments in this study and have also been used successfully to estimate ungulate impacts on recruitment in self-regenerating, stable aspen stands that have not burned (Rhodes et al., 2017a). Impacts of meristem removal on forest recruitment scales well across large landscapes especially when topography is taken into account (Rhodes et al., 2017a). We recommend using removal of apical meristems as an indicator of ungulate impact on aspen recruitment and suggest that ≈75% removal of apical meristems (Fig. 2) is an important threshold for height growth. We recommend less than 50% defoliation for successful aspen regeneration, depending on management targets for density (Fig. 2). Meristem removal measurements can offer a quick assessment, which warns managers of aspen regeneration problems due to ungulate herbivory. Also, ocular assessment of defoliation could replace surveys of meristem removal when time constraints exist. Both of these direct methods were superior to indirect measurements (fecal counts and camera counts) (Table 3) but indirect measurements still correlated with browse damage and can be valuable in identifying which ungulate species are having the greatest browse impact in a given area.

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