



Herbivory impacts of elk, deer and cattle on aspen forest recruitment along gradients of stand composition, topography and climate



Aaron C. Rhodes, Ho Yi Wan, Samuel B. St. Clair*

Department of Plant and Wildlife Sciences, Brigham Young University, Provo, UT 84602, USA

ARTICLE INFO

Article history:

Received 26 January 2017

Received in revised form 11 April 2017

Accepted 12 April 2017

Available online 29 April 2017

Keywords:

Aspen regeneration

Browsing

Fecal counts

Grazing

Populus tremuloides

Ungulate

ABSTRACT

The abundance and composition of large ungulate communities are changing dramatically across terrestrial ecosystems due to human activities. This has resulted in novel herbivory regimes that create strong top-down effects on biological communities, and can reduce ecosystem resilience. Biotic and abiotic conditions that influence the population structure and behavior of ungulate herbivores are highly variable across space and time, making it difficult to predict ungulate impacts across complex landscapes. Where multiple ungulate species co-exist, it can be challenging to differentiate species impacts on plant communities. We examined the effects of cattle, American elk, and mule deer on aspen regeneration and recruitment along gradients of forest composition and physiographic conditions in 3 National Forests of Utah, USA. Aspen regeneration and recruitment increased with winter precipitation, elevation and higher abundance of overstory aspen. Binned fecal count densities of elk, mule deer, and cattle showed strong inverse correlations with aspen height (elk: $r^2 = 0.83$; deer: $r^2 = 0.92$; cattle: $r^2 = 0.35$) and aspen recruitment (elk: $r^2 = 0.51$; deer: $r^2 = 0.59$). Aspen stem density was negatively correlated with elk ($r^2 = 0.35$) and cattle fecal densities ($r^2 = 0.71$). We found that 60% of the sites we surveyed had low ungulate activity and good aspen regeneration, 32% were intermediate use sites that warrant additional monitoring, and 8% of sites showed high ungulate use that exhibited aspen regeneration failure and lack of recruitment where targeted management is recommended. We conclude that ungulate impacts in aspen forests should be considered on a site by site basis and should primarily be evaluated based on the total abundance of the ungulate community with precipitation, elevation and stand composition as secondary factors.

© 2017 Elsevier B.V. All rights reserved.

1. Introduction

Ungulate herbivory strongly shapes plant evolution and plant community assembly (Augustine and McNaughton, 1998). Introduction of non-native ungulates, shifts in native ungulate populations, and extirpation of natural predators are changing the extent and intensity of ungulate herbivory across terrestrial ecosystems (Spear and Chown, 2009). These changes create novel herbivory regimes that can alter plant community composition and function (Augustine and McNaughton, 1998). Ungulate impacts on vegetation are highly variable across landscapes and are modified by both biotic factors (e.g. plant and animal community characteristics) (Veblen and Young, 2010) and abiotic conditions (e.g. topography, climate) (Long et al., 2014). This complexity makes it difficult to characterize ungulate impacts on plant community characteristics at broad spatial scales.

The impacts of ungulates on plant communities vary depending on the abundance, composition and behavior of the ungulate community (Koerner et al., 2014). Differential impacts of ungulate species are mediated by habitat selection and forage preference. Diet preference for plant species is related to differences in body size, physiology and nutritional requirements (Hanley, 1982; Koerner et al., 2014). However, in areas where multiple large ungulate species coexist, habitat use overlaps and competition for forage resources can intensify the detrimental effects of ungulate herbivory on palatable plant species (Augustine and McNaughton, 1998). Early successional plant species that form the foundation of plant community development tend to be more palatable (Coley et al., 1985) and are likely susceptible to the damaging effects of changing ungulate communities.

Across the continental forests of the northern hemisphere, aspen spp. (*Populus tremuloides* and *Populus tremula*) are early successional tree species of high ecological value. However, decline of aspen forests across portions of its North American range has uncovered vulnerabilities to stressors including ungulate herbivory

* Corresponding author at: 293 WIDB, Provo, UT 84602, USA.

E-mail address: stclair@byu.edu (S.B. St. Clair).

that threaten the long-term sustainability of these forest systems (Frey et al., 2004). Aspen is an important food source for several large mammal species including elk, deer and cattle. A growing abundance of these ungulate species in forest landscapes has increased herbivory pressure across aspen's range (Frey et al., 2004; Seager et al., 2013). With the populations structures of multiple ungulate species overlapping and changing, it has been difficult to evaluate the impacts of individual ungulate species on forest regeneration and recruitment.

Ungulates select habitat in order to maximize energy and nutrient acquisition efficiency (Hanley, 1982), avoid predation (Gervasi et al., 2013) and optimize thermoregulation in adverse climate conditions (Long et al., 2014). Mixed-aspen conifer forests vary in overstory stand composition from aspen dominance, to a mixed condition and finally to conifer dominance in late successional stages. These differences in forest stand characteristics create diverse habitat conditions that may influence patterns of aspen utilization by ungulates (Rogers and Mitanck, 2014). Early successional aspen forests are preferred habitat for multiple species of ungulates (Peterson and Peterson, 1992; Beck et al., 2006) which may lead to higher browsing of regenerating aspen.

Climate and physiographic conditions may also modify the effects of ungulate herbivory (Smith et al., 2011a). Variability in precipitation can strongly alter the behavior of ungulates and modify plant community sensitivity to herbivory (Young et al., 2013). Reductions in snowpack changes the timing and intensity of ungulate herbivory of regenerating aspen forests (Martin and Maron, 2012; Mysterud and Austrheim, 2014). There is evidence that aspen is susceptible to higher rates of insect herbivory, and disease in drier conditions (Dudley et al., 2015), but less is known about how weather patterns influence ungulate herbivory of aspen.

Topography alters ungulate herbivory patterns by altering habitat use due to variation in terrain ruggedness and forage selectivity related to differences in plant palatability (Augustine and Derner, 2014). Higher light availability increases aspen's resilience and tolerance to mammalian herbivory (Lindroth and St. Clair, 2013; Wan et al., 2014). Therefore, light gradients due to terrain slope and aspect may alter aspen's susceptibility to ungulate herbivory. Also, areas of steep slopes, or rocky terrain pose higher foraging costs for ungulates, and may influence foraging behavior (Long et al., 2014). Extreme relief or ruggedness often provide refuge from ungulate herbivory for preferred forage species (Banta et al., 2005). Despite the well-studied abiotic influences on selection of palatable plants, there are relatively few studies that have examined both the abiotic and biotic factors underlying patterns of ungulate herbivory.

The majority of research examining ungulate impacts on aspen regeneration (aspen < 150 cm) and recruitment (aspen ≥ 150 cm) has occurred in the initial stage of forest succession following disturbance (Seager et al., 2013). However, even in the mid to late stages of aspen forest succession, aspen continues to regenerate and recruit, producing multi-aged stands (Kurzel et al., 2007) that increase resilience to ecological stress (Smith et al., 2011b). Poor recruitment of young aspen stems due to ungulate herbivory is thought to increase vulnerability to drought and competitive exclusion by conifers (Frey et al., 2004; St. Clair et al., 2013; Rogers and Mitanck, 2014). We know much less about how ungulate herbivory shapes regeneration and recruitment success in mid to late stages of stand succession than in post-disturbance (i.e. fire) conditions. This is a critical knowledge gap because the vast majority of aspen forests exist in mid to late stages of stand succession.

The objective of this study was to characterize the influence of ungulate herbivory on aspen regeneration and recruitment patterns of intact forests across gradients of physiographic conditions, climate and forest stand composition at a regional scale. We tested three hypotheses: (1) Aspen regeneration and recruitment decrease with ungulate community abundance with the impacts

of elk, deer and cattle varying due to differences in their physiology and anatomy; (2) aspen regeneration and recruitment is lower in early succession, aspen dominated stands due to higher levels of ungulate use and herbivory; (3) climate and physiographic conditions affect aspen recruitment with greater winter precipitation and south facing slopes increasing regeneration and recruitment success.

2. Materials and methods

2.1. Study area

This study included 92-paired sites (184 total stands) located across the Manti-La Sal, Fishlake, and Dixie National Forests of Central and Southern Utah, USA (Fig. 1). Sites were selected that had adjacent aspen dominant and mixed aspen-conifer stands >100 m in diameter (identified by satellite imagery), and at least 50 m from roads. Each paired site consisted of an aspen dominant stand (>90% aspen) adjacent to a mixed aspen-conifer stand with approximately 50:50 aspen-conifer that provided a contrast in stand composition. The point-quarter method was used to determine overstory tree species composition, and stand density (Pollard, 1971). We defined mature overstory trees as those with greater than or equal to 8 cm in diameter at breast height. Aspen dominant stands averaged 93% ± 2 (SD), ranging from 90% to 100% overstory aspen density, and mixed stands averaged 43% ± 2 (SD) ranging from 15% to 60% overstory aspen density. Average tree density in aspen dominant and mixed aspen-conifer stands were 1250 ± 135 and 1540 ± 188 per hectare respectively.

Study sites had slopes ranging from 4% to 52% and elevations ranging from 2600 m to 3200 m, which represents the middle to upper portion of aspen's elevation range in the mountains of the western U.S. (Peterson and Peterson, 1992). The adjacency of the paired stands helped limit pairwise variation in aspect, slope, and precipitation. The study sites were grouped into 8 geographic sub-regions based on mountain ranges where they occur: Manti, Fishlake, Monroe Mt., Pavant, Tushar, Markagunt, Aquarius and La Sal (Fig. 1). We used ecoregions separated by mountain range in order to characterize variation in aspen regeneration and ungulate communities across the study region.

2.2. Ungulate fecal counts

In July 2012, we established one 50 m × 2 m belt transect in each stand, at least 20 m from the stand edge. We randomly selected the direction of each belt transect and marked both end points with 60 cm grade stakes and GPS waypoints. In each transect, we surveyed for fecal counts of American elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and cattle (*Bos taurus*) (Neff, 1968). We used the following criteria for counting current 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 was cleared from the plots after being surveyed. We conducted the fecal surveys in July 2012, and July 2013. 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. Fecal counts were used as a proxy for ungulate use.

2.3. Characterization of aspen regeneration

In each 50 m × 2 m belt transect mentioned above we surveyed aspen sucker regeneration and recruitment. We measured height, density and recruitment of regenerating aspen. For our study, we

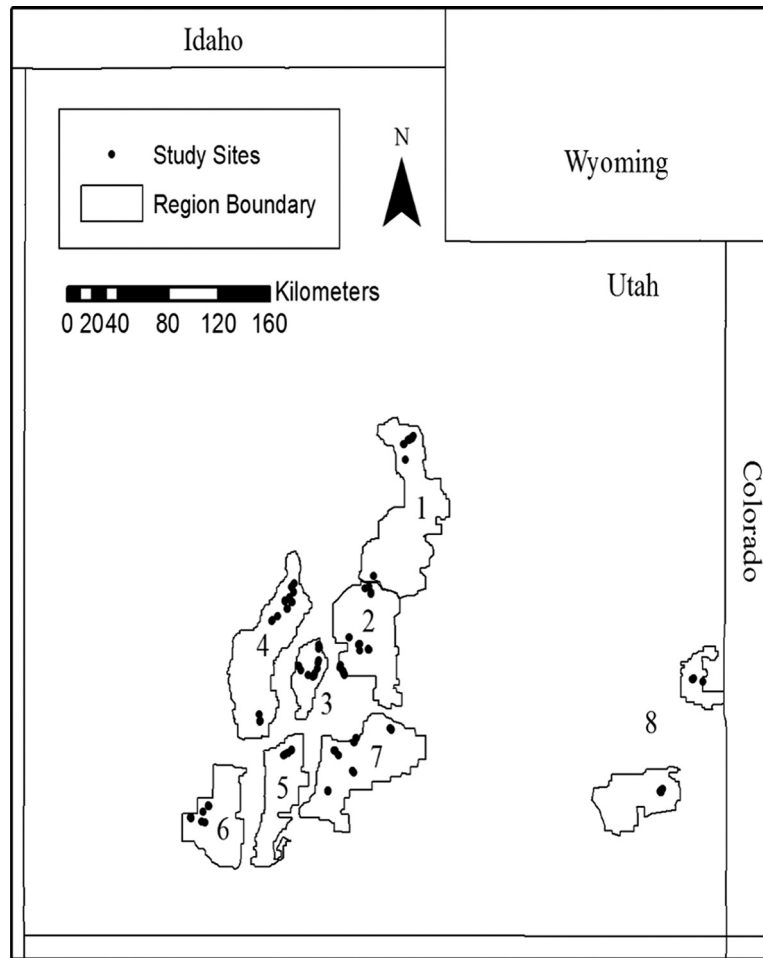


Fig. 1. Map of the extent of the study sites across central and southern Utah. Paired study sites in adjacent mixed and aspen dominant stands are marked with a single dot. The 8 mountain ranges are marked with numbers: (1) Manti, (2) Fishlake, (3) Monroe Mt., (4) Pavant, (5) Tushars, (6) Markagunt, (7) Aquarius, (8) La Sal.

defined an aspen sucker as being <150 cm in height and emerging independently from the ground (unbranched above ground level) within the transect. We considered aspen stems to be recruiting when they ranged in height from 150 cm to 200 cm tall. Recruitment was defined in this way because that is the height at which aspen usually begins to escape ungulate herbivory (Lindroth and St. Clair, 2013).

Browse impact 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; Wan et al., 2014). Aspen suckers with multiple subleaders were quite common, and the entire stem was considered browsed if all meristems were removed. 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).

2.4. Topography

We characterized topography by associating our GPS site waypoints with remotely sensed data from a 30 m × 30 m digital elevation model (USGS DEM, 2013) of Utah. From this DEM we extracted slope, aspect and elevation and related these to our study sites using ArcMap 10.1. Aspect was defined as either north or south aspect where 0° to <90° and >270° to 360° was considered north and 90° to 270° was considered south. We compared north

and south because we were interested in the influence of aspect on insolation and microclimate effects.

We used the standard deviation of slope extracted from the 30 m DEM as an index for terrain ruggedness. 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). We used model selection (comparing AICc values from univariate models) to identify the most appropriate moving window size (number of neighboring pixels used to calculate standard deviation of slope) for each pellet count. We used a 5 × 5 moving window based on comparison of other sizes using multimodel inference. (Grohmann et al., 2011).

2.5. Precipitation

We used PRISM (Daly et al., 2009) to extract temperature and precipitation data at the study sites. We considered two seasons of interest; winter given that snow pack is thought to protect aspen at higher elevation from over winter (January, February, March) herbivory (Peterson and Peterson, 1992) and spring (April, May, June) herbivory where precipitation may favor aspen growth. Thirty year averages ranged from 514 to 994 mm across our sites, providing a fairly wide gradient of precipitation. Annual precipitation across the sites averaged 429 ± 9 mm, 359 ± 10 mm, and 433 ± 10 mm in 2011, 2012, and 2013 respectively. Average maximum temperature for the winter period was 2 °C in 2012 and 4 °C in 2013, and for summer was 16 °C in both 2012 and 2013. We

used multimodel inference to pick the best precipitation and temperature estimator for our data set, and found prior winter precipitation and temperature to fit best. It is important to note that other precipitation and temperature measurements may influence aspen regeneration metrics, but we do not include them here.

2.6. Statistical analysis

To address our first and third hypotheses, we conducted a global analysis of aspen regeneration response to fecal counts as a proxy for ungulate activity, stand composition, precipitation, temperature and topographical variables. These variables were included as fixed effects in the mixed-effects linear models with mean aspen height, aspen density, mean aspen browse percent, and recruitment density designated as response variables. For these models (except for recruitment, explained below), we used paired sites (aspen and mixed) nested within ecoregions as the random effects structure and then used a top-down strategy of selection for fixed effects and all two-way interactions using likelihood ratio (maximum likelihood) tests (Zuur et al., 2009). Three way interactions were not tested given the high parameter size and limited sample size. Paired plots were used to test for multicollinearity. We found winter and spring precipitation to be collinear (>0.7 , Pearson's r), so only winter precipitation was used in the analysis. R-squared values for linear mixed-effects models were calculated through the MuMIn package by the methods of Nakagawa and Schielzeth (2013).

Recruitment (aspen ≥ 150 cm) was best modeled using a zero-inflated negative binomial distribution for the error structure. We considered time and region to be fixed effects for the zero-inflated models. We removed the least significant fixed effects by using a step-down approach with likelihood ratio tests to find an optimal model. We present Spearman's Rank correlation (ρ) of observed versus predicted values for our top model (Potts and Elith, 2006).

To test our first and second hypotheses, we pooled ungulate fecal counts into bins and modeled their mean effect on the aspen regeneration across all regions and years. Jenks natural breaks were used to find ten appropriate bins of fecal counts for elk, mule deer, and cattle (Jenks, 1967). We calculated the average and standard errors of height, recruitment, density and browse percent within those bins. We then conducted a weighted linear regression for each regeneration metric and recruitment across those bins. We then summed all ungulate fecal counts into bins and repeated the weighted linear regression to account for the entire ungulate community. All analyses were conducted using the program R (R Core Team, 2013), and packages nlme for mixed effects models, MuMIn for comparing multiple models through maximum likelihood, pscl for the zero-inflated model (Zeileis et al., 2008; Barton, 2015; Pinheiro et al., 2015).

3. Results

3.1. Global model summary

The optimal aspen height model included mule deer and cattle fecal counts, stand type and sampling year as fixed effects ($r^2 = 0.14$) (Table 1). Suckering density was best accounted for by elevation, with no other fixed effect included in the optimal model ($r^2 = 0.11$, $p < 0.01$, Table 1). The optimal model for aspen browse percent included elk fecal counts, stand type, and sampling year ($r^2 = 0.08$, $p < 0.01$, Table 1). Antecedent winter precipitation, summed ungulate fecal counts, and aspect provided the best explanation of recruitment of aspen suckers ($\rho = 0.13$, $p = 0.02$)

(Table 1). There were no significant two-way interactions between explanatory variables for any of the models.

3.2. Hypothesis 1: Ungulate effects on aspen regeneration and recruitment

Across all study sites 52% of aspen suckers exhibited evidence of being browsed by ungulates. Cattle and mule deer reduced aspen height by 1.1 cm and 0.6 cm per fecal count 100 m^{-2} , respectively (Table 1). Browse impact of aspen increased 0.4% per elk pellet group 100 m^{-2} (Table 1). There was a reduction of 4 aspen recruits ha^{-1} per pellet group of any ungulate species (Table 1).

In our binned regression analysis elk, deer and cattle fecal counts showed strong relationships, with measures of aspen regeneration and recruitment (Fig. 2). For each elk pellet group per 100 m^{-2} there was a 1.2 cm drop in aspen height ($r^2 = 0.83$, $p < 0.01$), 4.7 fewer aspen recruits ha^{-1} ($r^2 = 0.51$, $p = 0.01$), 33 fewer aspen suckers ha^{-1} ($r^2 = 0.35$, $p < 0.01$), and a 0.53% increase in browse impact ($r^2 = 0.60$, $p < 0.01$). For each deer pellet group per 100 m^{-2} , aspen height was reduced by 0.93 cm ($r^2 = 0.92$, $p < 0.01$) and 4.8 fewer aspen recruited ha^{-1} ($r^2 = 0.59$, $p < 0.01$). Each cattle fecal count per 100 m^{-2} was associated with a 0.85 reduction in aspen height ($r^2 = 0.35$, $p = 0.05$), and 103 fewer aspen suckers ha^{-1} ($r^2 = 0.71$, $p < 0.01$).

When fecal counts of all elk, deer and cattle were summed, the average aspen height was reduced by 0.75 cm per fecal count, and average recruitment was reduced by 3 recruits ha^{-1} (Fig. 3). Based on natural breaking points observed in the data, we categorized the number of sites into low, medium, or high use areas, based on reductions in both height and recruitment as a function of ungulate fecal counts (Fig. 3a and b). The analysis indicates that 60% of the 184 study stands were low use areas (≤ 8 fecal counts per 100 m^2), 32% were medium use ($8 < x \leq 26$ fecal counts 100 m^{-2}), and 8% of the sites were high use (>26 up to 71 fecal counts 100 m^{-2}) (Fig. 3d).

3.3. Hypothesis 2: Stand composition effects

Aspen suckers in mixed stands experienced 5% greater browse impact than those in aspen stands (Table 1). Aspen suckers in mixed stands were 5.2 cm shorter than aspen suckers in aspen stands (Table 1). Stand composition was not an important fixed effect for Aspen sucker density and recruitment did not vary significantly due to overstory stand composition (Table 1).

3.4. Hypothesis 3: effects of climate and topography

Southern aspects had as much as 3-fold greater aspen recruitment than northern aspects (Fig. 4).

Antecedent winter precipitation was positively correlated with aspen recruitment (Fig. 4b).

Elevation was positively correlated with aspen sucker density such that for each 100 m increase in elevation there was a 405 ± 120 increase in aspen sucker density ha^{-1} ($\chi^2 = 16$, $p < 0.01$) (Table 1). Browse impact was not correlated with topography or climate. Aspen regeneration and recruitment were not significantly related to terrain ruggedness or slope in any model.

4. Discussion

4.1. Overview

This study examined the effects of multiple ungulate species on aspen regeneration and recruitment across gradients of forest composition, climate, and topography in forests of central and southern

Table 1

Fixed effects for each of 4 models for aspen regeneration are presented. Height, density, browse %, and recruitment are in bold with the full model r^2 or rho presented on the same line. Under each model title are the fixed effects that were in the optimal model with their corresponding beta estimates \pm standard error, χ^2 and Z statistics for mixed effects models and zero-inflated models respectively, and their corresponding p -value.

Fixed effects	Beta estimate \pm SE	Statistic	p -value	Full model
Height		χ^2		$r^2 = 0.14$
Cattle	-1.1 ± 0.30 cm	12	<0.01	
Deer	-0.6 ± 0.19 cm	37	<0.01	
Mixed stand	-5.2 ± 2.0 cm	6	0.02	
Year (2013)	-12.7 ± 2.1 cm	32	<0.01	
Density		χ^2		$r^2 = 0.11$
Elevation	405 ± 120 ha $^{-1}$	16	<0.01	
Browse%		χ^2		$r^2 = 0.08$
Elk	$0.4\% \pm 0.2\%$	3.4	0.04	
Mixed Stand	$5\% \pm 1.4\%$	9	<0.01	
Year (2013)	$-6\% \pm 1.4\%$	3	<0.01	
Recruitment		Z		Rho = 0.13
Count model μ_i				
Cattle + Deer + Elk	-4 ± 1 ha $^{-1}$	-3.9	<0.01	
Lag Winter Precip.	0.8 ± 0.35 ha $^{-1}$	2.3	0.02	
South Aspect	65 ± 21 ha $^{-1}$	3.1	<0.01	
Zero Inflation Model π_i				
Elevation	-55 ± 2	2.7	<0.01	
Lag Winter Precip.	2 ± 0.7	2.8	<0.01	
Year (2013)	87 ± 37	2.3	0.02	

Utah. We found that ungulates have density dependent impacts on aspen regeneration and recruitment. Large variation in aspen regeneration across sites, as shown by low r^2 (Table 1), was likely influenced by genetic factors and physiographic conditions (Smith et al., 2011a, 2011b). By statistically binning variation across sites we were able to more clearly identify ungulate effects on aspen regeneration success (Figs. 2 and 3). Our first hypothesis that regeneration and recruitment decreases with ungulate abundance and that the impacts of elk, deer and cattle differ was partially supported. We found that aspen regeneration and recruitment was inversely correlated with ungulate abundance but there was less evidence that the impacts of elk, deer and cattle differed. In other words, increasing ungulate abundance of any species resulted in fairly similar linear reductions in aspen regeneration and recruitment vigor (Fig. 2). Studies that have considered differential effects of elk, deer and cattle species have also observed significant impacts by each species (Bork et al., 2013; Walker et al., 2015). Our second hypothesis that aspen regeneration and recruitment success would be higher in aspen dominant vs. mixed stands was partially supported. Browse impact was higher and aspen were shorter in mixed stands, but these metrics did not translate into detectable differences in regeneration or recruitment densities (Table 1). Our third hypothesis was supported in which elevation, aspect, and winter precipitation each contributed to some of the variation in aspen regeneration and recruitment success (Table 1). Finally, there was strong variation in aspen regeneration and recruitment success across the geographic range of our study.

4.2. Ungulate effects on aspen regeneration and recruitment

The results demonstrate that greater fecal counts of ungulates were negatively correlated with aspen regeneration and recruitment (Fig. 2). The data clearly show that high abundance of ungulates can drive complete aspen recruitment failure (Fig. 3b). The data indicate that 8% of the sites had fecal densities at levels that caused aspen regeneration and recruitment failure with 32% of sites showing intermediate impacts where recruitment potential is delayed or at some level of risk (Fig. 3d). These areas of high ungulate impact showed impacts that are consistent with other studies where intense ungulate herbivory caused aspen regenera-

tion and recruitment failure in intact stands (Kaye et al., 2005). The majority of our study sites (60%) had aspen that were regenerating well and showed good evidence of recruitment into the overstory (Fig. 3d). These sites had lower ungulate activity, as measured by ungulate fecal counts. Our study shows a gradient of impact on aspen regeneration and recruitment that varies strongly according to the density dependence of the ungulate community (Fig. 3). Our regression models show clear linear relationships between binned fecal counts and aspen regeneration responses. However, given that our sampling was not truly random, these proportions may not be representative of the entire statistical population. These models should allow for a more targeted management approach for controlling the damaging effects of ungulate on aspen forests.

Across North America, there have been many examples where one ungulate species in particular was thought to be driving aspen regeneration failure. For example, aspen loss has been attributed to deer on the Kaibab plateau (Leopold et al., 1947), elk in Yellowstone (Ripple and Beschta, 2007), and cattle in Alberta (Kaufmann et al., 2014). Our results suggest that any one of these species independently, or a mixed community of ungulates, when at sufficient abundance can drive aspen regeneration failure (Fig. 3c). Our results indicate that the mean herbivory impacts of elk, deer and cattle on aspen are fairly similar on a per fecal count basis (Fig. 2) suggesting there is little need to separate out species influences to accurately assess the potential impacts of the whole ungulate community. Therefore, characterizing impact of the ungulate community using fecal surveys is both a simple and accurate way of assessing vulnerabilities of aspen forest to ungulate herbivory (Fig. 3b) (Wan et al., 2014).

4.3. The role of stand composition in ungulate impacts on aspen

The species composition of forest stands can alter aspen regeneration success (Bartos, 2001; St. Clair et al., 2013) and influence ungulate impacts on forest understories (Mason et al., 2010). We found aspen suckers in mixed stands to be browsed 5% more and were 5.2 cm shorter on average than suckers in aspen stands (Table 1). Higher browse of aspen suckers in mixed aspen-conifer stands may be due to reductions in growth rates and defense of

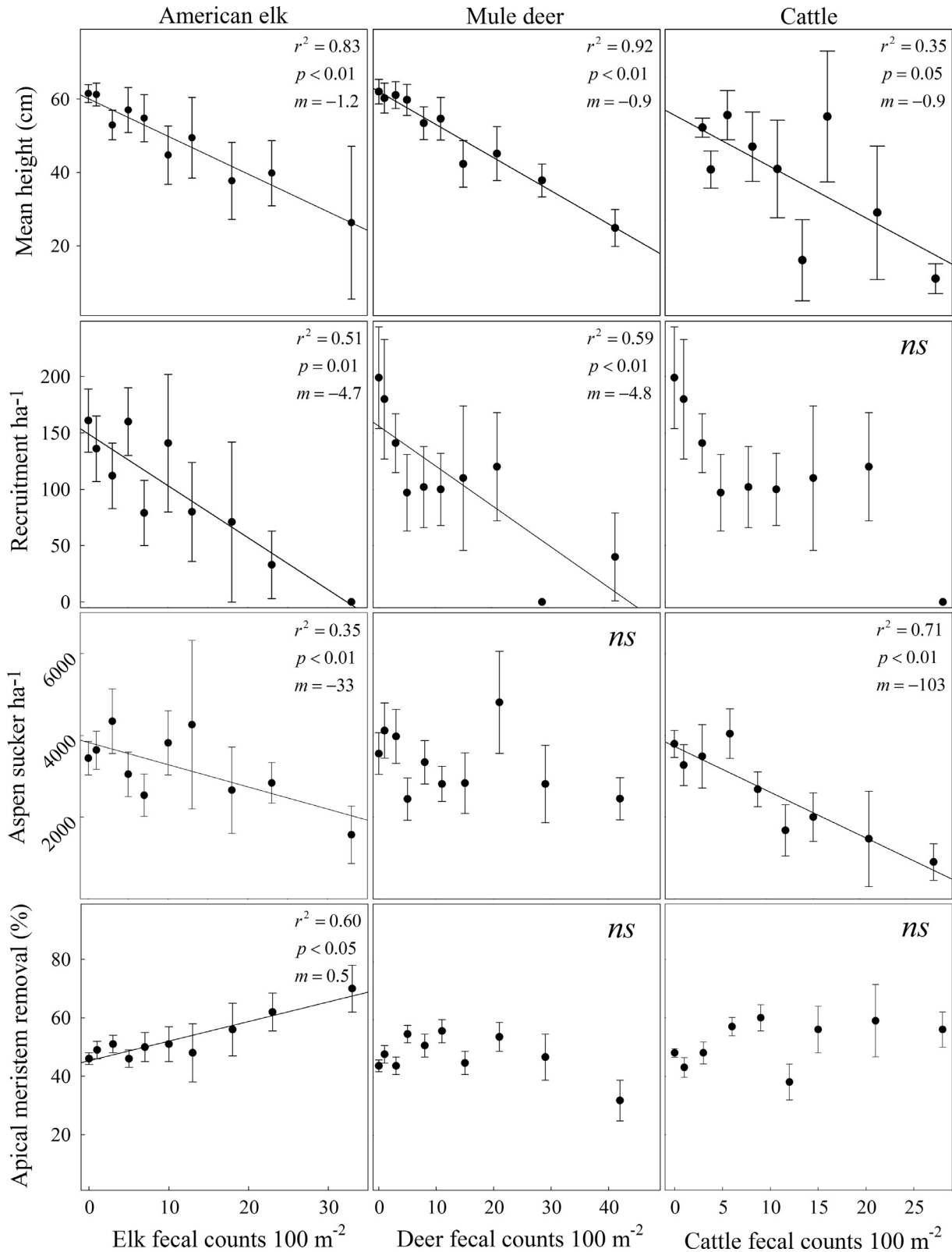


Fig. 2. Binned means at the Jenk's natural breaks are presented with their associated error bars (\pm standard error). Weighted linear models that were statistically significant have their r^2 , p , and slope (m) values. Non-significant models are denoted with "ns". Height is reported in cm, recruitment is per hectare, aspen suckering is per hectare, and browse percent are presented for American elk, mule deer, and cattle fecal counts.

aspen due to lower light conditions (Wan et al., 2014). Also, late successional aspen forest communities tend to support less palatable species (Peterson and Peterson, 1992), which may increase preference for aspen (Villalba et al., 2014). Also, vegetation type

and structure influence ungulate habitat use due to perception of predation risk (Gervasi et al., 2013). While ungulate effects on browse use and height in mixed stands was only slightly larger, these impacts may be compounded if aspen in mixed stands are

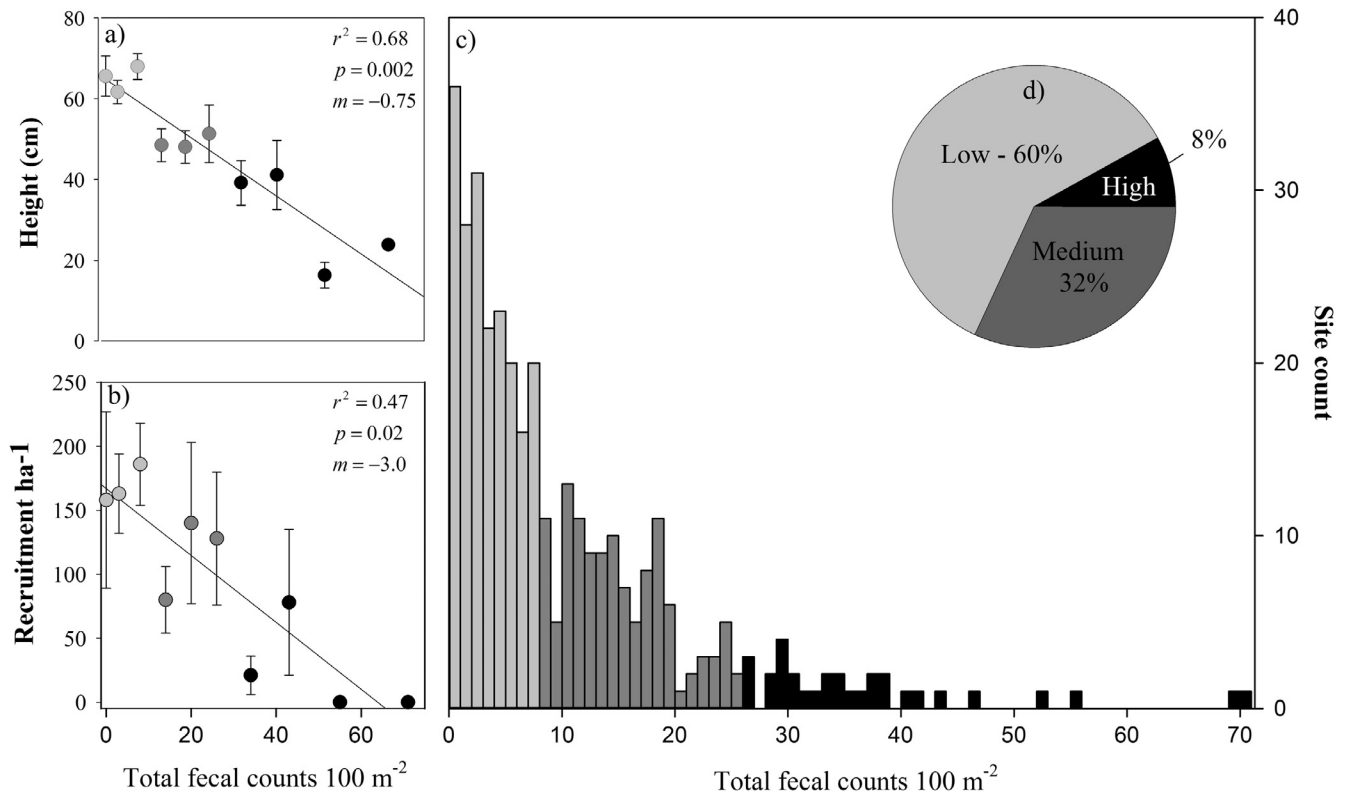


Fig. 3. Regression analysis of (a) aspen height and (b) aspen recruitment as a function of binned fecal counts summed for elk, deer and cattle. Error bars represent the standard error around the mean of that bin. (c) A frequency histogram indicates the number of sites that have fecal counts ranging from 0 to 71. (d) A pie chart of the proportion of sites in low, medium, and high categories of ungulate use. In all four graphics, gray scale shading is matched and represents low (light gray), medium (dark gray) and high (black) reductions in aspen height and related to increasing fecal count densities. The three categories were defined based on visual breaks in the data.

continuously utilized year over year. This is consistent with other studies showing that long-term ungulate impacts on aspen regeneration and recruitment grow as conifer abundance increases in forest stands (Kaye et al., 2005; Rogers and Mittanck, 2014). High overstory conifer abundance also decrease the vigor of aspen regeneration after disturbance (Smith et al., 2011a), which contributes to long-term loss of aspen stands (Worrall et al., 2013). Our results, suggest that ungulates reduce aspen recruitment potential in both aspen dominant and mixed stands. However, effects are slightly stronger in mixed stands, which may accelerate succession to conifers.

4.4. The role of topography and climate

Topography plays a role in the success of aspen regeneration patterns (Smith et al., 2011a) due to its influences on moisture, temperature and animal behavior (Long et al., 2014). In our analysis, higher elevation and southern aspect tended to have positive effects on aspen regeneration density and recruitment, respectively, but had no effect on height or browse percent (Table 1). Southern aspect provides higher insolation in the northern hemisphere, which increases aspen vertical growth rates and stimulates defense chemistry expression against herbivory (Wan et al., 2014). Further, warmer soil temperature on southern aspect can trigger aspen suckering (Peterson and Peterson, 1992) and faster growth rates when water is non-limiting. Therefore, increased aspen regeneration and recruitment on southern exposures may be partially driven by higher resistance and tolerance to browse pressure by ungulates (Lindroth and St. Clair, 2013).

Elevation contributed to increases in aspen regeneration density in our models (Table 1). Rogers and Mittanck (2014) also found

higher regeneration density with increasing elevation. This positive relationship tracks well with suitable elevation habitat range for aspen. Predictions for aspen habitat suitability suggest aspen at lower elevation are susceptible to changing climate conditions (Worrall et al., 2013). For example, aspen at lower elevation are susceptible to climate related stress including drought (Worrall et al., 2013) and temperature extremes (Martin and Maron, 2012; Worrall et al., 2013). Also, deeper snowpack found at higher elevations can reduce overwinter browsing, and improves water relations throughout the growing season (Martin and Maron, 2012; Mysterud and Austrheim, 2014). Drier conditions characteristic of lower elevations in our study area can also increase susceptibility to disease, and insect herbivory (Dudely et al., 2015), and appears to be true for mammalian herbivory.

Terrain ruggedness can influence aspen regeneration (Rogers and Mittanck, 2014), but, our analysis suggests that it was less important than other ecological factors. Refuge for plant communities from ungulates due to terrain ruggedness likely happens at a limited spatial scale, whether on a steep slope (Zegler et al., 2012), or in refuge islands provided by boulders (Banta et al., 2005). Since our analysis was conducted at broad spatial scales and regeneration and recruitment did not vary with terrain ruggedness in our models it supports the idea that the effects of terrain ruggedness on ungulate herbivory occur at smaller spatial scales (Zegler et al., 2012).

Precipitation can have an important role in explaining aspen regeneration success (Dudely et al., 2015), and mediates ungulate impacts on aspen (Martin and Maron, 2012). We observed that antecedent winter precipitation increased aspen recruitment success (Table 1, Fig. 4). Winter precipitation likely affects aspen recruitment in two ways. First, drier conditions increase aspen sus-

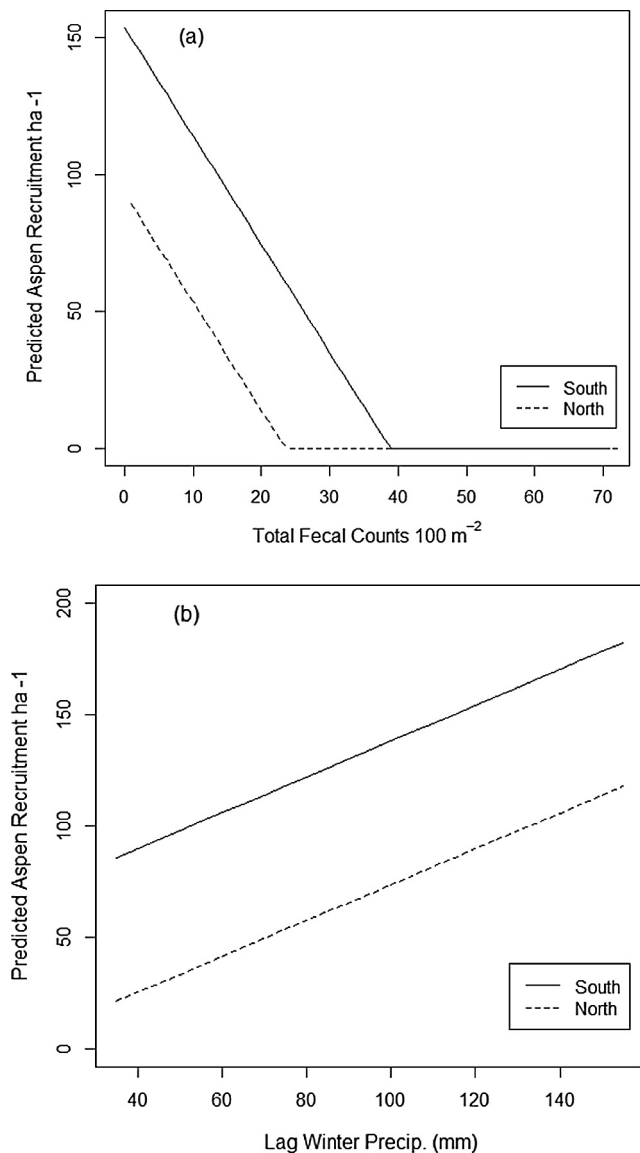


Fig. 4. Using the zero inflation count model intercept and beta coefficients, this graph presents in panel (a) the predicted mean number of aspen recruitment ($150 \text{ cm} \geq x \geq 200 \text{ cm}$) per hectare across the observed total animal fecal counts (Cattle + Deer + Elk) and in panel (b) the observed lag winter precipitation (mm). The solid line represents the predicted values at southern aspect and the dashed line represents the predicted mean at northern aspect. Lag winter precipitation was held at the mean 90 mm. Animal fecal counts (Cattle + Deer + Elk), were held at the median = 6.

ceptibility to hydraulic failure, disease, and insect herbivory (Worrall et al., 2013; Dudely et al., 2015). Second, greater snowpack reduces ungulate herbivory by decreasing winter browsing (Martin and Maron, 2012) and by improving forage quality of other understory plant species the following summer (Mysterud and Austrheim, 2014). Differences in palatability between grasses, forbs, and aspen played an important role in selection for aspen in cafeteria trials (Villalba et al., 2014), suggesting the greater availability of other forage sources due to more favorable weather patterns can decrease ungulate preference for aspen.

4.5. Ecological implications

Shifts in ungulate community abundance and composition across terrestrial ecosystems are altering plant communities. In some aspen forests, there is evidence that ungulate use is reducing

aspen recruitment (Kaye et al., 2005; Rogers and Mittanck, 2014) which diminishes resilience to environmental stressors of younger cohorts due to low phenotypic diversity (Smith et al., 2011b). Our study suggests that areas of high ungulate use are failing to recruit (Fig. 3), and that is driven primarily by ungulate abundance.

Changing climate conditions pose new challenges for managing ungulate herbivory especially for more palatable, early successional species, like aspen (Worrall et al., 2013). Our data show that antecedent winter precipitation has an important impact on the recruitment of aspen (Fig. 4). In areas where winter precipitation regimes are changing, aspen recruitment and resilience may be at risk. Our study provides further evidence that climate will affect the range and distribution of aspen (Worrall et al., 2013; Dudley et al., 2015), through reduction in aspen recruitment. Incorporating an understanding of the influence of physiographic, climate and habitat conditions into management of ungulates can improve plant community resilience to herbivory. Because environmental conditions that interact with ungulate herbivory are shifting due to climate change (Worrall et al., 2013), it is critical that we understand these relationships with greater precision.

While much research has looked at ungulate impact on aspen regeneration after fire or timber harvest (Seager et al., 2013; Kaufmann et al., 2014), few studies have examined how ungulate herbivory affects recruitment in mature aspen stands. We show that aspen regenerating in both aspen dominant and seral aspen-conifer mixed stands are under herbivory pressure (Table 1). High rates of ungulate herbivory may increase rates of succession through selective herbivory of palatable early successional species (Randall and Walters, 2011) and reduce stand resilience to disturbance by reducing densities of young cohorts (Smith et al., 2011a). While the effects of heavy ungulate use on post-disturbance sites are generally dramatic and rapid, the majority of aspen forests exist in an intact state, and the ungulate effects on regeneration and recruitment in these stands is less obvious. However, our data demonstrate when ungulate impacts regeneration in aspen dominant and mixed stands they may have important implications for stand resilience to drought and other environmental stressors (Smith et al., 2011b).

4.6. Conclusions and management implications

Our study explored ungulate use across large environmental and spatial gradients, and found that ungulate herbivory negatively influences aspen regeneration and recruitment. Management of aspen regeneration should include multivariate monitoring that includes both biotic and abiotic factors, and consider temporal and spatial variability in ungulate use on a site by site basis. Care should be taken to avoid broad extrapolation from studies with small ranges of time and space in their experimental design.

Based on our pellet surveys the majority of the region evaluated in our study (60%) experienced low ungulate use with good aspen regeneration. Intermediate ungulate use was observed in 32% of the sites surveyed, which could warrant further monitoring. Only 8% of the study areas experienced severe regeneration and recruitment problems due to high ungulate use and should be the focus of targeted management (Fig. 3). Based on our data it appears that fecal counts can be used as a good proxy of ungulate use to identify areas that may be prone to aspen recruitment failure. Fencing, targeted hunts and other techniques (Seager et al., 2013) can be used effectively in high ungulate use stands to stimulate recruitment and the development of multi-cohort aspen stands. Management of ungulates in aspen forests should be considered on a site by site basis and should primarily be evaluated based on the abundance of the total ungulate community.

Authors' contributions

SS conceived the ideas and designed methodology; AR AND HW collected the data; AR and SS analysed the data; AR and SS led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.04.014>.

References

- Augustine, D.J., McNaughton, S.J., 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *J. Wildl. Manage.*, 1165–1183.
- Augustine, D.J., Derner, J.D., 2014. Controls over the strength and timing of fire–grazer interactions in a semi-arid rangeland. *J. Appl. Ecol.* 51 (1), 242–250.
- Banta, J.A., Carson, J.P., Royo, A.A., Kirschbaum, C., 2005. Plant communities growing on boulders in the Allegheny National Forest: evidence for boulders as refugia from deer and as a bioassay of overbrowsing. *Nat. Areas J.* 25 (1), 10–18.
- Barton, K., 2015. MuMIn: Multi-Model Inference. R package version 1.15.1. <<http://CRAN.R-project.org/package=MuMIn>>.
- Bartos, D.L., 2001. Landscape dynamics of aspen and conifer forests. USDA Forest Service Proceedings RMRS-P-18.
- Beck, J.L., Peek, J.M., Strand, E.K., 2006. Estimates of elk summer range nutritional carrying capacity constrained by probabilities of habitat selection. *J. Wildl. Manage.* 70 (1), 283–294.
- Bork, E.W., Carlyle, C.N., Cahill, J.F., Haddow, R.E., Hudson, R.J., 2013. Disentangling herbivore impacts on *Populus tremuloides*: a comparison of native ungulate and snags in Canada's Aspen Parkland. *Oecologia* 173, 895–904.
- Coley, P.D., Bryant, J.P., Chapin, F.S., 1985. Resource availability and plant antiherbivore defense. *Science* 230 (4728), 895–899.
- Daly, C., Conklin, D.R., Unsworth, M.H., 2009. Local atmospheric decoupling in complex topography alters climate change impacts. *Int. J. Climatol.* <http://dx.doi.org/10.1002/joc.200>.
- Dudley, M.M., Burns, K.S., Jacobi, W.R., 2015. Aspen mortality in the Colorado and southern Wyoming Rocky Mountains: extent, severity, and causal factors. *For. Ecol. Manage.* 353, 240–259.
- Frey, B.R., Loeffers, V.J., Hogg, E. (Ted), Landhäusser, S.M., 2004. Predicting landscape patterns of aspen dieback: mechanisms and knowledge gaps. *Can. J. For. Res.* 34 (7), 1379–1390.
- Gervasi, V., Sand, H., Zimmermann, B., Mattisson, J., Wabakken, P., Linnell, J.D.C., 2013. Decomposing risk landscape structure and wolf behavior generate different predation patterns in two sympatric ungulates. *Ecol. Appl.* 23 (7), 1722–1734.
- Grohmann, C.H., Smith, M.J., Riccomini, C., 2011. Multiscale analysis of topographic surface roughness in the Midland Valley, Scotland. *IEEE Trans. Geosci. Remote Sens.* 49 (4), 1200–1213.
- Hanley, T.A., 1982. The nutritional basis for food selection by ungulates. *J. Range Manag.* 35, 146–151.
- Jenks, G.F., 1967. The data model concept in statistical mapping. *Int. Yearbook Cartograp.* 7, 186–190.
- Jones, B.E., Burton, B., Tate, K.W., 2005. Effectiveness monitoring of aspen regeneration on managed rangelands – a monitoring method for determining if management objectives are being met in aspen communities R5-EM-TP-004. USDA, Forest Service, Pacific Southwest Region, Vallejo, CA, US.
- Kaufmann, J., Bork, E.W., Alexander, M.J., Blenis, P.V., 2014. Effects of open-range cattle grazing on deciduous tree regeneration, damage, and mortality following patch logging. *Can. J. Forest Res.-Revue Canadienne De Recherche Forestiere* 44 (7), 777–783.
- Kaye, M.W., Binkley, D., Stohlgren, T.J., 2005. Effects of conifers and elk browsing on quaking aspen forests in the central Rocky Mountains, USA. *Ecol. Appl.* 15 (4), 1284–1295.
- Koerner, S.E., Burkepile, D.E., Fynn, R.W.S., Burns, C.E., Eby, S., Govender, N., Hagenah, N., Matchett, K.J., Thompson, D.I., Wilcox, K.R., Collins, S.L., Kirkman, K. P., Knapp, A.K., Smith, M.D., 2014. Plant community response to loss of large herbivores differs between North American and South African savanna grasslands. *Ecology* 95 (4), 808–816.
- Kurzel, B.P., Veblen, T.T., Kulakowski, D., 2007. A typology of stand structure and dynamics of Quaking aspen in northwestern Colorado. *For. Ecol. Manage.* 252 (1–3), 176–190.
- Leopold, A., Sows, L.K., Spencer, D.L., 1947. A survey of over-populated deer ranges in the United States. *J. Wildl. Manage.* 11, 162–183.
- Lindroth, R.L., St. Clair, S.B., 2013. Adaptations of quaking aspen (*Populus tremuloides* Michx.) for defense against herbivores. *For. Ecol. Manage.* 299, 14–21.
- Long, R.A., Bowyer, R.T., Porter, W.P., Mathewson, P., Monteith, K.L., Kie, J.G., 2014. Behavior and nutritional condition buffer a large-bodied endotherm against direct and indirect effects of climate. *Ecol. Monogr.* 84 (3), 513–532.
- Mason, N.W.H., Peltzer, D.A., Richardson, S.J., Bellingham, P.J., Allen, R.B., 2010. Stand development moderates effects of ungulate exclusion on foliar traits in the forests of New Zealand. *J. Ecol.* 98 (6), 1422–1433.
- Martin, T.E., Maron, J.L., 2012. Climate impacts on bird and plant communities from altered animal–plant interactions. *Nat. Clim. Change* 2 (3), 195–200.
- Mysterud, A., Austrheim, G., 2014. Lasting effects of snow accumulation on summer performance of large herbivores in alpine ecosystems may not last. *J. Anim. Ecol.* 83 (3), 712–719.
- Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R² from generalized linear mixed-effects models. *Meth. Ecol. Evol.* 4(2), 133–142.
- Neff, D.J., 1968. The pellet-group count technique for big game trend, census, and distribution: a review. *J. Wildl. Manage.* 32 (3), 597–614.
- Peterson, E.B., Peterson, N.M., 1992. Ecology, management and use of aspen and balsam poplar in the prairie provinces, Canada. Special Report 1. Forestry Canada, Northwest Region, Northern Forestry Centre, Edmonton, Alberta, vol. 1, 252 p.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team 2015. *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-120, <<http://CRAN.R-project.org/package=nlme>>.
- Pollard, J.H., 1971. On distance estimators of density in randomly distributed forests. *Biometrics* 27 (4), 991–1002.
- Potts, J.M., Elith, J., 2006. Comparing species abundance models. *Ecol. Model.* 199 (2), 153–163.
- Core Team, R., 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. 3-900051-07-0, <<http://www.R-project.org/>>.
- Randall, J.A., Walters, M.B., 2011. Deer density effects on vegetation in aspen forest understoreys over site productivity and stand age gradients. *For. Ecol. Manage.* 261 (3), 408–415.
- Ripple, W.J., Beschta, R.L., 2007. Restoring Yellowstone's aspen with wolves. *Biol. Cons.* 138 (3–4), 514–519.
- Rogers, P.C., Mittanck, C.M., 2014. Herbivory strains resilience in drought-prone aspen landscapes of the western United States. *J. Veg. Sci.* 25 (2), 457–469.
- Seager, S.T., Eisenberg, C., St. Clair, S.B., 2013. Patterns and consequences of ungulate herbivory on aspen in western North America. *For. Ecol. Manage.* 299, 81–90.
- Smith, E.A., O'Loughlin, D., Buck, J.R., St. Clair, S.B., 2011a. The influences of conifer succession, physiographic conditions and herbivory on quaking aspen regeneration after fire. *For. Ecol. Manage.* 262, 325–330.
- Smith, E.A., Collette, S.B., Boynton, T.A., Lillrose, T., Stevens, M.R., Bekker, M.F., Eggett, D., St. Clair, S.B., 2011b. Developmental contributions to phenotypic variation in functional leaf traits within quaking aspen clones. *Tree Physiol.* 31 (1), 68–77.
- Spear, D., Chown, S.L., 2009. Non-indigenous ungulates as a threat to biodiversity. *J. Zool.* 279 (1), 1–17.
- St. Clair, S.B., Cavard, X., Bergeron, S.B., 2013. The role of facilitation and competition in the development and resilience of aspen forests. *For. Ecol. Manage.* 299, 91–99.
- United States Geological Survey digital elevation model 2013. Data available from the U.S. Geological Survey. <<http://eros.usgs.gov/elevation-products>>.
- Veblen, K.E., Young, T.P., 2010. Contrasting effects of cattle and wildlife on the vegetation development of a savanna landscape mosaic. *J. Ecol.* 98 (5), 993–1001.
- Villalba, J.J., Burritt, E.A., St. Clair, S. B., 2014. Aspen (*Populus tremuloides* Michx.) intake and preference by Mammalian Herbivores: the role of plant secondary compounds and nutritional context. *J. Chem. Ecol.* 40(10), 1135–1145.
- Walker, S.C., Anderson, V.J., Fugal, R.A., 2015. Big game and cattle influence on aspen community regeneration following prescribed fire. *Rangeland Ecol. Manage.* 68 (4), 354–358.
- Wan, H.Y., Rhodes, A.C., Clair, S.B.S., 2014. Fire severity alters plant regeneration patterns and defense against herbivores in mixed aspen forests. *Oikos* 123 (12), 1479–1488.
- Worrall, J.J., Rehfeldt, G.E., Hamann, A., Hogg, E.H., Marchetti, S.B., Michaelian, M., Gray, L.K., 2013. Recent declines of *Populus tremuloides* in North America linked to climate. *For. Ecol. Manage.* 299, 35–51.
- Young, H.S., McCauley, Douglas J., Helgen, K.M., Goheen, J.R., Otarola-Castillo, E., Palmer, T.M., Pringle, R.M., Young, T.P., Dirzo, R., 2013. Effects of mammalian herbivore declines on plant communities: observations and experiments in an African savanna. *J. Ecol.* 101 (4), 1030–1104.
- Zeileis, A., Kleiber, C., Jackson, S., 2008. Regression Models for Count Data in R. *J. Statistical Software* 27(8). <<http://www.jstatsoft.org/v27/i08/>>.
- Zegler, T.J., Moore, M.M., Fairweather, M.L., Ireland, K.B., Fule, P.Z., 2012. *Populus tremuloides* mortality near the southwestern edge of its range. *For. Ecol. Manage.* 282, 196–207.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. *Mixed Effects Models and Extensions in Ecology With R*. Springer, NY, USA.