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Differential effects of cattle, mule deer, and elk herbivory on aspen forest regeneration and recruitment

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ABSTRACT

The abundance and composition of ungulate herbivore communities are changing globally, which can impact the resilience and function of Earth's ecosystems. Impacts from herbivory are compounded in areas where multiple ungulates overlap, which is common in forest ecosystems. The objective of this study was to examine the differential and combined effects of ungulate communities (deer, elk, and cattle) on aspen forest recruitment after fires that occurred in 2012. Eight sets of differential ungulate exclosures, monitored by camera traps, were established across three National Forests in Utah. We identified the differential effect of each of three ungulate species using fencing that allowed for deer-only, native ungulate only (deer and elk), all ungulates and a complete ungulate exclosure. Over a three year period (2013–2016) we quantified ungulate species impacts on aspen height, density, and browse rates using camera trap photos. Ungulate activity was nearly 10-fold higher in two National Forests compared to the third, and gradually decreased over time. Meristem removal by ungulates in unfenced plots across sites averaged 60% which we identified as a critical threshold point for aspen recruitment failure. All three ungulate species had significant and similar effects on aspen regeneration success, but when adjusted for differences in estimated forage intake (animal unit months), differential impacts became apparent (deer > elk > cattle). We estimated that 4 cattle per camera^{-1} day^{-1} and 2.5 deer or elk per camera^{-1} day^{-1} was sufficient to reach the critical recruitment threshold of 60% removal of apical meristems. We conclude that ungulates species differentially influence aspen regeneration and recruitment, and that ungulate browsing above 30% meristem removal impairs aspen recruitment with recruitment failure occurring above 60% meristem loss.

1. Introduction

Native and non-native ungulate populations can influence plant community development and reduce ecosystem stability (Côté et al., 2004, Spear and Chown, 2009). The frequency and magnitude of ungulate herbivory can define thresholds for forest regeneration and recruitment (Strand et al., 2009, Wisdom et al., 2006). Ungulate herbivory has particularly strong effects on plant recruitment in post-disturbance environments (Augustine and McNaughton, 1998). Ungulate influence on plant communities are often most intense in the early stages of forest succession following disturbance (Augustine and McNaughton, 1998, Wisdom et al., 2006). However, quantifying ungulate influence on forest regeneration and identifying forest recruitment thresholds by ungulate species are confounded by overlapping habitat and diet of multiple ungulate species.

What herbivores choose to eat is mediated by complex physiological and environmental cues (Hanley, 1982; Hoffman, 1989; Long et al., 2014). Interspecific differences in ungulate anatomy drive differences in forage preference (Clauss et al., 2010), providing a framework for understanding ungulate forage selection and their differential impacts on forest recruitment and succession. Ungulate species are generally divided into three classes; "concentrate feeders", "intermediate feeders", and "grass and roughage eaters", hereafter referred to as: browsers, mixed feeders, and grazers (*sensu lato* Hoffman, 1989). Body size, mouth anatomy, stomach type (ruminant vs. cecal), and rumino-reticular volume are among the major physiological features that influence diet strategy in ungulates (Hanley, 1982). Grazers generally have large body size and/or large rumino-reticular volume both of which favor selection of lower quality forage like grasses. Browsers generally have smaller rumino-reticular volume and must select for high-quality forage that passes relatively quickly though the digestive system. Browsers, given their smaller mouth size and need for higher quality forage, should select palatable portions of tree species such as meristems and leaf tissue. Mixed feeders fall between the two previously described types with intermediate anatomical features and diets (Hoffman, 1989). This conceptual framework predicts differential

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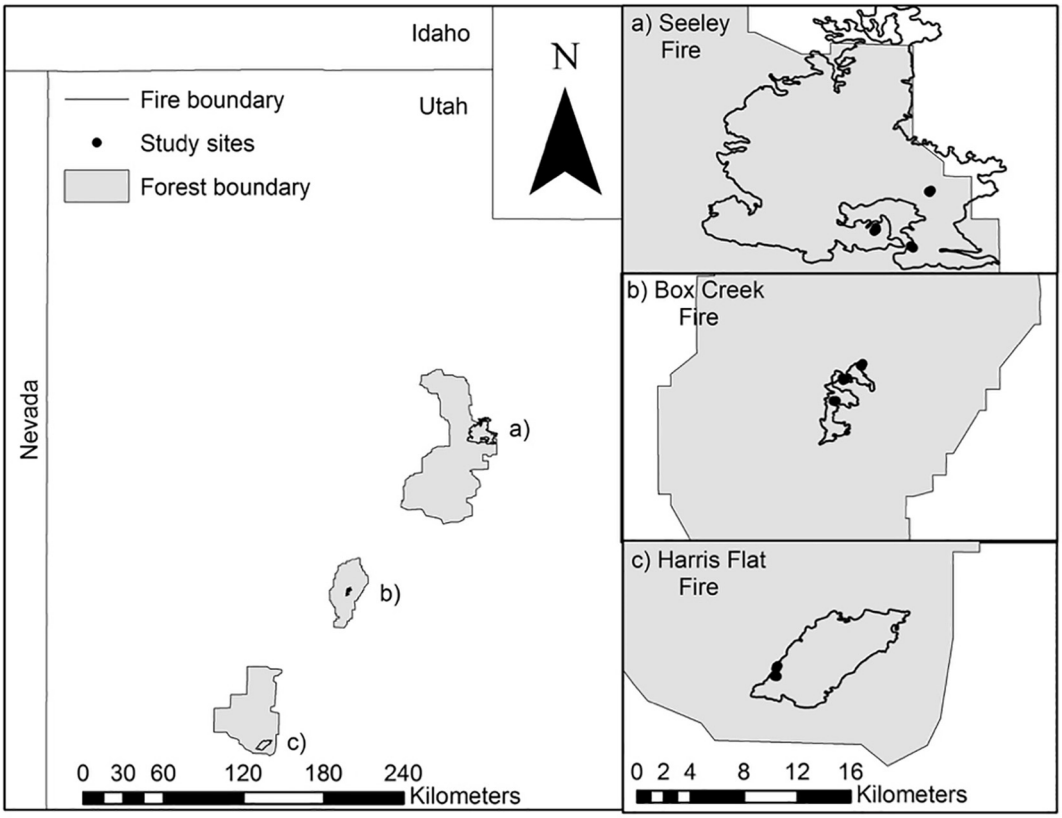

Fig. 1. Map of the study area. This map shows the larger study area encompassing central and southern Utah. National forest boundaries are in gray and fire perimeters are in black. Three inset maps display black dots at the study sites. At each a four block differential fencing treatment is located. All three inset maps use the same scale.

herbivory impacts on forest regeneration as follows: browser > mixed feeder > grazer (Clauss et al., 2010; Hoffman, 1989).

Aspen is a foundation tree species (Ellison et al., 2005) that provides habitat for hundreds of plant and animal species (Peterson and Peterson, 1992). Aspen forests are preferred habitat for deer (*Odocoileus* spp.) and elk, (*Cervus canadensis*) (Beck et al., 2006) and are utilized by cattle (*Bos taurus)* due to the high productivity and forage quality in their understory (DeByle, 1985). Aspen forms the foundation of forest successional cycles in many montane and subalpine mixed conifer forests of the intermountain west of North America by regenerating through root suckering after fire (Calder and St. Clair, 2012; St. Clair et al., 2013). Regenerating aspen suckers are highly palatable and susceptible to ungulate herbivory (Seager et al., 2013) and high rates of ungulate herbivory can result in aspen regeneration and recruitment failure (Rhodes et al., 2017a). Therefore, identifying thresholds at which ungulate herbivory interferes with aspen recruitment is critical to identifying aspen regeneration success and its implication for the resilience of aspen ecosystems.

Quantifying the differential effects of multiple coexisting ungulate species is key to defining thresholds for successful aspen recruitment. Monitoring removal of apical meristems is a good indicator of ungulate effects on aspen regeneration and subsequent recruitment (Rhodes and St. Clair, 2018). Thresholds for aspen recruitment in self regenerating aspen forests not triggered by fire have been identified at or near 30% browse removal of apical meristems (Jones et al., 2005; Olmsted, 1979; Strand et al., 2009). However, there are no current estimates for browsing thresholds of aspen recruitment in post-fire conditions, and little quantification of interspecific contribution of individual ungulate species on aspen regeneration and recruitment (Bork et al., 2013). Aspen tolerance of and resistance to ungulate herbivory increases with greater burn severity (Wan et al., 2014a) and fire size (Wan et al., 2014b). Both burn severity and fire size are positively correlated with aspen suckering density and negatively correlated with ungulate influence (Smith et al., 2011; Wan et al., 2014a, 2014b). Therefore, aspen regeneration and recruitment thresholds in response to ungulate herbivory may differ in post-fire conditions dependent on the size and severity of fires.

The effect of ungulate herbivory on forest recruitment is influenced by multiple environmental factors (Dudley et al., 2015; Rhodes et al., 2017b) and can be highly variable in space and time (Rhodes et al., 2017a; 2017b). Topography is an important determinant of ungulate-aspen interactions due to its effects on temperature, precipitation and ungulate foraging behavior (Long et al., 2014; Rhodes et al., 2017b; Smith et al., 2011). Elevation covaries with temperature and precipitation and affects subsequent snowpack persistence and hydrology (Morán-Tejeda et al., 2013; Sospedra-Alfonso et al., 2016). Snowpack depth and persistence affects ungulate herbivory of aspen by limiting the movement and access of ungulates during the winter and spring periods (Brodie et al., 2012; Martin and Maron, 2012; Rhodes et al., 2017b). Moreover, aspen at lower elevations are subjected to warmer and drier conditions (Worrall et al., 2013) which can increase susceptibility to disease and herbivory (Dudley et al., 2015; Strand et al., 2009). Therefore, incorporating a measure of elevation and relative ungulate use across space and time provides a better mechanistic understanding of how ungulate species influence aspen regeneration and forest recruitment.

The central objective of this study was to quantify the individual and combined influence of mule deer, elk, and cattle on aspen regeneration and recruitment in complex, post-fire forest environments. We hypothesized that ungulate use of aspen, as measured by removal of apical meristems, would vary across burned landscapes and years post fire due to variability in ungulate visitation over space and time. Second, we hypothesized that aspen regenerating at lower elevations would experience lower height, density, recruitment and higher browse