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Long-term Protection from Heavy Livestock Grazing Affects Ponderosa Pine Understory Composition and Functional Traits[☆,☆☆]

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ABSTRACT

Making accurate predictions of plant community responses to grazing management is a major objective of rangeland ecology. Metrics such as species composition are site specific, whereas others such as functional groups and functional traits can be generalized across different rangeland types. We analyzed long-term (1912–1941) shifts in the understory community at five sites in a ponderosa pine (*Pinus ponderosa* P. & C. Lawson var. *scopulorum* Engelm.) forest when protected from heavy livestock grazing. We examined differences in total basal cover, species composition, species richness, functional group composition, and community-weighted mean (CWM) functional traits between heavily grazed and ungrazed areas in four time periods (1912, 1920, 1930, 1940). Total understory basal cover was greater in ungrazed than heavily grazed areas in 1920 but not in later time periods. Understory species composition diverged by 1930 and continued to differ in 1940. Functional group composition differed from 1920 onwards. In 1920 and 1930, C_3 graminoids declined more in relative abundance in heavily grazed than ungrazed areas. By 1940, forbs accounted for much more of the cover in heavily grazed than ungrazed areas. During the study period, CWM specific leaf area and foliar N_{mass} declined by 8% and 11%, respectively, in ungrazed quadrats, while CWM leaf dry matter content increased 8%. Leaf traits, but not maximum height or seed mass, demonstrated consistent and predictable responses to protection from heavy grazing. Herbaceous understory species with leaf traits that allow for slower resource acquisition became more abundant in response to protection from heavy grazing. Our results indicate that managers should expect to observe more rapid changes in functional group composition and leaf functional traits than in species composition and species richness following protection from heavy livestock grazing.

Introduction

Grazing by domestic ungulates is one of the most widespread forms of land use world-wide (Díaz et al., 2006). Research on the impacts of grazing (here, referring specifically to livestock grazing) has largely focused on understanding shifts in species composition (Milchunas and Lauenroth, 1993). However, this approach may have hindered a broader understanding of the processes underlying community-level responses to grazing because it does not allow for generalizations beyond a specific locality (Vesk and Westoby, 2001).

Given the degree to which land-use change impacts plant biodiversity (Chapin et al., 2000), understanding the functional consequences of grazing can improve management of rangelands. Identifying consistent shifts in plant functional strategies (as quantified by functional groups or plant traits) in response to grazing can improve regional and global models of vegetation dynamics (Díaz et al., 2006). While livestock grazing is one of the factors resulting in dramatic increases in tree density (Bakker and Moore, 2007) and shifts in plant community composition (Arnold, 1950; Cooper, 1960; Clary, 1975; Milchunas, 2006) across the Southwest US, relatively little attention has been given to functional responses following protection from heavy grazing (Arnold, 1955).

Plant functional classifications have received much attention from ecologists seeking predictable patterns in response to disturbance, particularly grazing (McIntyre et al., 1999). A classification

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based on life history strategies is common and has revealed a common pattern with increased grazing pressure favoring annual versus perennial plant species (Arnold, 1955; Milchunas and Lauenroth, 1993; McIntyre and Lavorel, 2001). Many classification schemes exist (Smith et al., 1997), including the well-established GFL classification of graminoids (G), nonleguminous forbs (F), and legumes (L) (Wright et al., 2006). Graminoids are often further refined by distinguishing between taxa with C_3 (cool season) and C_4 (warm season) photosynthetic pathways to reflect phenological differences and because utilization by grazers varies with grazing season (Smith, 1967).

A more recent alternative is to consider continuously distributed plant functional traits instead of categorical functional groups. Functional traits influence vegetation dynamics, community response to disturbance, and ecosystem function (Pakeman and Quested, 2004). Westoby (1998) proposed a leaf-height-seed (LHS) scheme that quantifies plant strategies by locating species in a three-dimensional trait space defined by specific leaf area (SLA), vegetative height, and seed mass. These traits play a central role in a plant's ability to capture resources, compete, and regenerate. The leaf economics spectrum represents a gradient of resource acquisition rates (Wright et al., 2004) and can be examined using a set of coordinated traits: SLA, leaf dry matter content (LDMC), and leaf nitrogen concentration (foliar N_{mass}) (Laughlin et al., 2010). Leaves with high SLA have low LDMC and high foliar N_{mass}; species with this set of coordinated traits tend to have high relative growth rates stemming from high net photosynthetic capacity (Reich et al., 1997; Wright et al., 2004). Maximum vegetative height at maturity primarily reflects a species' competitive ability. In ecosystems where light is limited, taller plants have the potential to realize faster growth rates due to their ability to intercept more light (Poorter et al., 2008). Seed mass reflects variation in a species' ability to disperse to and colonize sites. Seed mass also reflects a fundamental tradeoff between seed size and reproductive output. Larger-seeded species produce fewer seeds for a given reproductive effort; however, seedlings of these species have more reserves with which to establish in low-resource environments (Kitajima, 2002) and are better equipped to tolerate defoliation (Armstrong and Westoby, 1993).

Westoby (1999) related the LHS scheme to grazing response. He proposed that under heavy non-selective grazing, high SLA species should be at a competitive advantage due to faster regrowth. Taller species should decrease in abundance because they would receive more attention from livestock. Species that produce large quantities of small seeds should increase in abundance because heavy grazing would create many gaps in which seedling establishment could occur. These responses are based on the underlying concept that through the selective removal of plant material, grazing affects a plant's ability to capture resources, compete, and regenerate (Grime, 1977; Noy-Meir et al., 1989). As grazing intensity increases, selection is thought to favor less competitive species adapted to rapidly acquire resources under temporarily favorable conditions. Alternatively, by excluding grazing from the environment, competition for light and nutrients should increase.

Some prior work has examined the effects of grazing on plant traits. Vegetative height has long been a key functional trait thought to reflect a mechanism of grazing avoidance, with increased levels of grazing intensity consistently favoring shorter plants (Dyksterhuis, 1949; Arnold, 1955; Díaz et al., 2001; Díaz et al., 2006). Seed mass, SLA, foliar N_{mass}, LDMC, and leaf toughness have been used to understand and predict the impact of grazing because these traits are thought to reflect a general trade-off in growth versus defense (Moles and Westoby, 2004; Adler et al., 2004; Cingolani et al., 2005; Louault et al., 2005; Laliberté et al., 2012; Wesuls et al., 2012; Moreno García et al., 2014). Some researchers suggest that generalizations of grazing impacts described by plant traits may be difficult (Vesk and Westoby, 2001), whereas others suggest that plant species' responses to herbivory might be idiosyncratic with regard to LHS traits (Butterfield and Callaway, 2012). Nevertheless, Díaz et al. (2006) suggested reanalyzing existing species-based studies to evaluate trait-based responses to grazing.

Both compositional and trait-based approaches provide valuable information regarding rangeland responses to grazing. Where a functional trait-based approach has the potential to be more generalizable across rangeland types, species and functional group data are easier to collect and provide important site-specific information. Combining both can allow for a more comprehensive understanding of the effects of grazing on vegetation structure and function.

In this study, we reanalyzed data from a unique long-term study to determine vegetation responses to continued heavy livestock grazing and recovery patterns when livestock were excluded for 30 yr. Permanent chart quadrats were established in 1912 in heavily grazed ponderosa pine–bunchgrass forests in northern Arizona. About half of the quadrats continued to experience heavy grazing while the others were protected from livestock grazing and are hereafter referred to as being ungrazed. A subset of the quadrats were used to document the influence of increasing pine regeneration on perennial grass cover (Arnold, 1950), but no studies have been published that used them to examine the effects of excluding heavy grazing over time. To isolate the effects of grazing during the study period, we statistically controlled for overstory dominance, soil texture, and elevation among quadrats and over time. To date, this is one of the few long-term studies examining changes in species composition due to grazing in the ponderosa pine type of the Southwest (Arnold, 1950; Milchunas, 2006; Loeser et al., 2007).

We formulated three hypotheses on the basis of our understanding of grazing management during the study period. First, we hypothesized that ungrazed and continuously grazed communities would diverge in species composition and in functional group composition, and that these changes would result primarily from recovery by perennial graminoids in ungrazed areas because these species would have been at a competitive disadvantage under the heavy levels of grazing common before protection (Talbot and Hill, 1923; Arnold, 1955). Second, we hypothesized that species richness would be higher in ungrazed areas because the duration and intensity of grazing would limit richness in grazed areas to those species able to tolerate or avoid grazing. Third, we hypothesized that functional traits would diverge between ungrazed and grazed communities. Specifically, we hypothesized that ungrazed communities would exhibit 1) lower mean SLA, lower foliar N_{mass}, and higher mean LDMC because species with this set of coordinated traits would have a greater competitive advantage in less disturbed environments (Grime, 1977), 2) a higher mean vegetative height due to increased competition for light, and 3) greater seed mass because seedling establishment would be favored by species that produce larger seeds in low-light and lower-resource environments (Kitajima, 2002).

Methods

Study Area

Between 1870 and 1910, the Southwest experienced an unprecedented introduction of domesticated livestock as a result of Euro-American settlement of the region (Olberding et al., 2005; Milchunas, 2006). In 1914, national forests in Arizona issued grazing permits for 6 800 horses, 243 200 cattle, and 379 000 sheep (Hill, 1915). Although little information is available regarding specific stocking rates, it was widely recognized that the ponderosa pine–bunchgrass forests of northern Arizona were overstocked and grazing ranged