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Original Research

Livestock Exclusion Impacts on Oak Savanna Habitats—Differential Responses of Understory and Open Habitats☆

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ABSTRACT

Large grazing animals can have profound impacts on plant communities and soil properties; however, these impacts are not always uniform across or within regions. The distribution of features such as forage quality, water, or shade within a pasture can change the behavior of grazers and thus, the impact of their grazing. Where managed livestock grazing has been proposed as a conservation tool to enhance or maintain desirable plant communities, understanding how spatial variation between tree and intertree habitats within a savanna landscape affects the response of vegetation and soil properties to grazing will be critical for designing management plans for different sites. In this study, we used a previously established, long-term livestock grazing experiment in California oak [*Quercus* L.] savannas to investigate how the removal of grazing affected plant communities and soil characteristics underneath and outside of isolated tree canopies. In the oak understory, plant community composition shifted in response to livestock removal, largely due to a 68 − 400% increase in the relative cover of native species. Overall plant community composition in open grassland neighboring trees changed little in response to livestock grazing removal, yet we did see a decrease in species richness and diversity surrounding deciduous oaks as the dominance of the exotic annual *Bromus diandrus* Roth increased. The depth of plant litter increased 1 − 2 cm in both habitat types when livestock grazing was absent, along with minor changes in soil carbon, nitrogen, and bulk density. These results highlight how different habitat patches within savanna landscape can have varying responses to grazing removal and illustrate how challenging it will be to use grazing as a management tool to enhance the diversity of native species. In the oak understory, native species that are tolerant of herbivory may be absent or unable to coexist with non-native annual grasses. The abundance of understory habitat at a particular site may therefore be an important variable predicting the outcome of livestock grazing.

Introduction

Livestock grazing is one of the most widespread human land uses globally, with rangelands comprising approximately 51% of the world's land area (Heady and Child 1994). Large grazing animals, whether wild herds or domestic livestock, have significant effects on the ecosystems they occupy (Borer et al. 2014; Milchunas and Lauenroth 1993; Olff and Ritchie 1998). In many grassland and savanna habitats, herbivory by grazing mammals and its associated disturbances alter plant diversity and soil resources, as well as the spread or persistence of exotic species (Dorrough et al. 2007; McSherry and Ritchie 2013; Strum et al. 2015). Livestock grazing tends to reduce dominance by tall, competitive grasses and break up dense litter layers, resulting in positive effects on overall community diversity by favoring small-stature, broad-leaved plants (Díaz et al. 2007; Pakeman 2004). These effects on plant species are not always similar across local or regional environmental gradients (Cingolani et al. 2005; Koerner et al. 2014; Lunt et al. 2007; Osem et al. 2002). For example, Marty (2015) showed negative, positive, and neutral effects of grazing on native plant richness along a fine-scale moisture gradient in vernal pool grasslands. Understanding how local habitat influences grazing responses will be critical for land managers seeking to use grazing as a conservation tool.

Many local attributes of a rangeland affect the behavior of grazing ungulates within a pasture or rangeland, including the patchiness of forage, water, and shade (Adler et al. 2001; Chapman et al. 2007; Senft et al. 1985). Large, isolated trees in African savannas are important resources for wild and domestic grazing ungulates; understory forage is frequently of higher nutritional quality and dung deposition is higher beneath trees (Belsky 1992; Treydte et al. 2007; Treydte et al. 2010). Yet for many types of grasslands outside of Africa, we lack a clear understanding of how the presence of trees affects the impact of livestock.

Livestock grazing is a dominant land use within California oak [*Quercus* spp.] savannas and woodlands, and it has both directly and

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indirectly impacted the structure of these habitats. In California, > 80% of large properties (> 200 acres) within oak woodland are grazed by livestock (Huntsinger et al. 2010; Spiegal et al. 2016). Although oak trees are an important feature of California landscapes ecologically and socially (Davis et al. 2016; McClaran and Bartolome 1985), they have been extensively cleared and thinned since the arrival of Europeans (Huntsinger et al. 2010; Tyler et al. 2007), and in many cases, thinning took place for rangeland "improvement" (Frost et al. 1997). These losses and the introduction of many new species coincide with reductions in Native American burning across the California foothills (Anderson 2005), undoubtedly also affecting the relative distribution of oaks across the region. Oak recruitment has been episodic or rare over the past 2 centuries, maintaining the widespread decline in oak density across California savannas (McLaughlin and Zavaleta 2013; Zavaleta et al. 2007).

Previous evaluations of the effects of livestock grazing have focused mostly on open habitats (i.e., grasslands, or the grass- or herbaceous-dominated portions of savannas) and revealed mostly positive effects on species diversity and richness, particularly among native and nonnative forbs (Stahlheber and D'Antonio 2013; Bartolome et al. 2014, but see Bartolome and McClaran 1992). The oak understory, however, is often highly dominated by non-native annual grasses unpalatable to most domestic grazers once they reach anthesis, and thus these plant communities may respond differently (Callaway et al. 1991; Marañón and Bartolome 1993; Marañón et al. 2009; Stahlheber et al. 2015). In this study we took advantage of a long-term livestock grazing experiment established in 1995 (Tyler et al. 2008) to compare the effects of livestock removal on oak understory and open grassland communities. In particular, we asked 1) How does the removal of grazing affect the plant community composition in the oak understory compared with adjacent open grassland habitat, especially the richness and cover of native versus exotic species? and 2) How does the removal of grazing affect soil characteristics and the abundance of plant litter in these two habitat types?

Methods

Study Site

This study was conducted within Sedgwick Ranch (34°41′N, 120°2′W), a 2 388-ha reserve operated by the University of California, Santa Barbara since 1995. The climate is Mediterranean, with hot, dry summers and cool wet winters. The mean annual precipitation at this location is 380 mm, although high interannual variation in rainfall is a defining characteristic of the region. Precipitation for the "water years" (defined as 1 September to 31 August of the following year) during the study (2007–2008, 2008–2009) was 403 and 332 mm, respectively (Table S1; available online at http://dx.doi.org/10.1016/j.rama.2016.10.003). The water year before the survey period began (2006–2007) was particularly dry (167 mm). The study area has not burned since establishment of the reserve.

We gathered data in an area called the "Mesa," a mostly level, uplifted Pleistocene terrace with fine, sandy loam soils in the Positas series (fine, smectitic, thermic Mollic Palexeralfs). Before creation of the University of California Reserve in 1995, livestock grazing for beef production was the dominant use of this site, and there is no evidence of prior cultivation or plowing (Tyler et al. 2008). Livestock were removed from the majority of the reserve following its establishment, and grazing only continued in fenced pastures in the context of experimental work. Populations of native bunchgrasses such as *Stipa pulchra* Hitchc., *Stipa cernua* Stebbins & Love, and *Poa secunda* J. Presl occur at this site, interspersed within grasslands dominated by the exotic annual grasses including *Bromus diandrus* Roth, *Bromus hordeaceus* L., *Avena barbata* Pott ex Link, and *Avena fatua* L., which originated in the Mediterranean and arrived with European colonists to the region. Similar to many sites in California, several species of oak tree occur throughout the grassland. Here the dominant savanna trees are the evergreen *Quercus agrifolia* Née (coast live oak) and the deciduous *Quercus lobata* Née (valley oak). The deciduous *Quercus douglasii* Hook. & Arn. (blue oak) is also present, though less common in savanna than the other two oak species.

Vegetation and Soil Survey

In the early spring of 2008 and 2009 (the beginning of the growing season in March − April), we surveyed the surroundings of 10 *Q. lobata* and 11 *Q. agrifolia* divided among grazed and ungrazed locations (5 each for ungrazed locations, 5 grazed *Q. lobata*, and 6 grazed *Q. agrifolia*). The grazing pastures were set up in 1995 as part of a long-term experiment on oak recruitment. Each pasture included one or more 50 × 50 m exclosures, and each exclosure included an adult oak tree at the center (see Tyler et al. 2008 for more information on experimental design). Some of our surveyed ungrazed oaks were inside these exclosures (four *Q. lobata* and two *Q. agrifolia*), while other ungrazed trees were located outside but adjacent to the fenced pastures. Fire and grazing history for these trees is identical to the exclosures within pastures. For both the grazed and ungrazed locations, oaks were haphazardly selected according to the following criteria: 1) located on predominantly flat terrain and 2) isolated from neighboring oaks by > 10 m on at least three sides. At this site, there was no evidence that *Q. agrifolia* and *Q. lobata* occurred on separate substrates or in response to an environmental gradient (discussed in Stahlheber et al. 2015). The stocking rate for the study period was ~45 head each year with paddock size ranging from 10 to 30 acres. Timing and duration of grazing varied depending on grass productivity and height, but typically cattle were introduced into the pastures in January, rotated among pastures, and removed in late May (Tyler et al. 2008).

At each oak tree, we sampled vegetation and soils in 1 × 1 m survey quadrats, equally divided between the understory and surrounding open grassland (defined as > 5 m beyond the canopy drip line). Quadrats were located along transects from the understory to open grassland along azimuths of 0, 90, 180 and 270° relative to true north (Fig. S1; available online at http://dx.doi.org/10.1016/j.rama.2016.10.003) with four plots sampled in understory and four in open grassland in the vicinity of each tree. Survey quadrats were marked in the field and surveyed in both years. Within each quadrat, we recorded the percent cover of all plant species present and the depth of dead plant material on the soil surface 10 cm within each of the four plot corners (including dead annual grass thatch and oak leaf litter). Relative cover (as a proportion of total cover) was used in our subsequent analysis, as we allowed individual plant species cover to total > 100% where there was overlap in canopies. The average total cover of both tree species and pasture types (grazed vs. ungrazed) was close to 100%, however, so using relative cover should not change our interpretation of the data.

We collected soil cores (5.4-cm diameter) to 15-cm depth next to each quadrat in late May to early June of 2008. In the laboratory, gravimetric soil moisture was determined for subsamples taken from all soil cores. Whole cores were air-dried and weighed to calculate bulk density. Next, we sieved each core to determine the percent rocks and coarse organic material (> 2 mm) by weight. We measured soil pH using an Orion AquaPro 9156APWP electrode (Thermo Fisher Scientific Inc., Waltham, MA), and electroconductivity (μS/mL) was tested using an ECTestr 11 + (Oakton Instruments, Vernon Hills, IL). Both pH and electroconductivity were determined on a 3:1 (water:dried soil) slurry. Total carbon and nitrogen were measured using an NA 1500 Series 2 analyzer (Fisons Instruments, Beverly, MA). Subsamples of soil were sent to the University of California Davis Analytical Laboratory for measurements of exchangeable K, Na, Ca, and Mg.

Data Analysis

Since the same survey plots were measured in each year, we used repeated-measures models to examine the influence of oak species, grazing, year, and their interactions on various attributes of the plant community. The oak understory and open grassland were considered