Received: 17 September 2020 | Accepted: 19 May 2021

DOI: 10.1111/1365-2745.13871

Journal of Ecology
BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Context-dependent effects of shifting large herbivore assemblages on plant structure and diversity

Devyn A. Orr[1] | An Bui[1] | Maggie Klope[1] | Ian M. McCullough[2] | Michelle Lee[1] | Carina Motta[1] | Isabella Mayorga[3] | Kelli Konicek[1] | Hillary S. Young[1]

[1]Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA, USA

[2]Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI, USA

[3]School for Environment and Sustainability, University of Michigan, Ann Arbor, MI, USA

Correspondence
Devyn A. Orr
Email: devynorr@gmail.com

Funding information
Division of Environmental Biology, Grant/Award Number: 1900502; Hellman Foundation; Sage and Sea Audubon Society; U.S. Department of Defense, Grant/Award Number: National Defense Science and Engineering Graduate

Handling Editor: Eric Allan

Abstract

1. Despite wide recognition of the importance of anthropogenically driven changes in large herbivore communities—including both declines in wildlife and increases in livestock—there remain large gaps in our knowledge about the impacts of these changes on plant communities, particularly when combined with concurrent changes in climate. Considering these prominent forms of global change in tandem enables us to better understand controls on savanna vegetation structure and diversity under real-world conditions.
2. We conducted a field experiment using complete and semi-permeable herbivore exclosures to explore the difference in plant communities among sites with wild herbivores only, with cattle in addition to wild herbivores, and with no large herbivores. To understand variation in effects across climatic contexts, the experiment was replicated at three locations along a topoclimatic gradient in California. Critically, this is the first such experiment to compare cattle and wildlife impacts along an environmental gradient within a single controlled experiment.
3. Vegetation structure responded strongly to herbivore treatment regardless of climate. Relative to the isolated effects of wildlife, exclusion of all large herbivores generally increased structural components related to cover and above-ground biomass while the addition of cattle led to reductions in vegetation cover, litter, shading and standing biomass. Furthermore, wildlife had a consistent neutral or positive effect on plant diversity, while the effect of livestock addition was context dependent. Cattle had a neutral to strongly negative effect at low aridity, but a positive effect at high aridity. These results suggest that (a) herbivore effects can override climate effects on vegetation structure, (b) cattle addition can drive different effects on diversity and (c) herbivore effects on diversity are modulated by climate.
4. *Synthesis*. Our results illustrate very distinctive shifts in plant communities between two realistic forms of change in ungulate herbivore assemblages—livestock addition and large herbivore losses—particularly for plant diversity responses, and that these responses vary across climatic contexts. This finding has important implications for the management and protection of plant biodiversity given that over a quarter of the Earth's land area is managed for livestock and climate regimes are changing globally.

KEYWORDS
biodiversity, cattle, climate, community structure, context dependence, herbivory, livestock, plant–herbivore interactions, wildlife

1 | INTRODUCTION

Accelerating human-caused changes in biodiversity at both local and global scales have prompted concern over the functional consequences of species losses in natural ecosystems (Forbes et al., 2019; Young et al., 2016). Globally, large-bodied ungulate herbivores play an important role in top-down control of vegetation dynamics and are key determinants of vegetation structure and biodiversity in grasslands and savannas (Collins et al., 1998; Jia et al., 2018; Knapp et al., 1999; McNaughton et al., 1989; Olff & Ritchie, 1998; Young et al., 2013). These impacts on plant communities have been shown to have profound functional effects that cascade throughout ecosystems, altering processes as varied as productivity (Charles et al., 2017; Cleland et al., 2019; Fay et al., 2015; Stevens et al., 2015), disease transmission (Keesing et al., 2013; Young et al., 2014), and soil and plant elemental pools and fluxes (Crowther et al., 2019; Firn et al., 2019; Forbes et al., 2019; Sitters et al., 2020). However, wild ungulate herbivores are disappearing from many ecosystems worldwide through land use changes, habitat loss, fragmentation and overexploitation (Collen et al., 2009; Dirzo et al., 2014; Prins, 2000; WallisDeVries et al., 1998), while being simultaneously introduced to others, predominantly as livestock (Barnosky, 2008; Knapp et al., 1999), but also as feral invasives (e.g. *Sus scrofa*, Mack & Antonio, 1998; Vitousek, 1986). Livestock now account for 60% of all mammalian life on Earth, equalling approximately a trillion kilograms in biomass (Bar-On et al., 2018). This is exponentially increasing large herbivore densities from pre-human baselines across the globe (Barnosky, 2008), particularly in arid and semi-arid grasslands which compose over a third of the world's rangelands (de Haan et al., 1997). This trajectory is likely to continue to accelerate as landscapes become increasingly human-dominated (Figure 1).

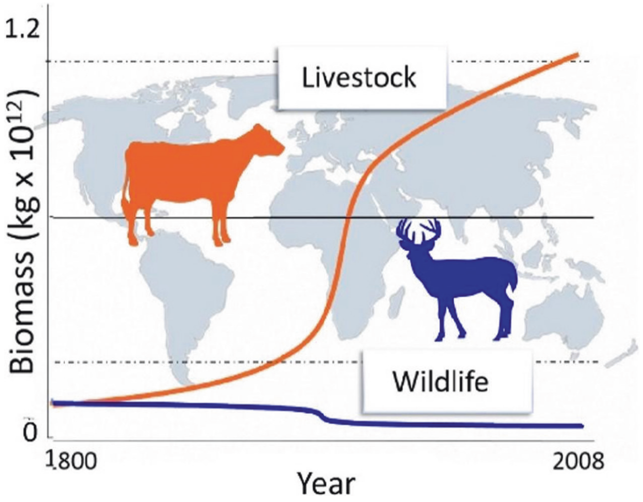

FIGURE 1 While wildlife is in decline globally (blue line), this has been more than compensated for by massive increases in livestock. Data from Barnosky (2008) and Bar-On et al. (2018)

Understanding the ramifications of such shifts in large herbivore assemblages requires empirical investigation of these density- and identity-driven impacts on plant communities, a need that has been highlighted by recent syntheses (e.g. Forbes et al., 2019; Jia et al., 2018). Many manipulative experimental studies have demonstrated causal linkages between presence of wild and domestic ungulates and changes in herbaceous plant communities (e.g. Bakker et al., 2006; Borer et al., 2014; Gao & Carmel, 2020; Koerner et al., 2018), yielding tremendous insight into the effects of both isolated defaunation (the complete loss of large-bodied wildlife), as well as real-world change scenarios in which livestock are the dominant large herbivores on the landscape (Porensky et al., 2013; Veblen et al., 2016; Young et al., 2013). Collectively, these experiments reflect realistic patterns of herbivore composition change now occurring throughout most grassland ecosystems—specifically, the additive or compensatory role of livestock in locations where herbivore assemblages are already depauperate relative to late Pleistocene communities (Porensky et al., 2013; Veblen et al., 2016; Young et al., 2013).

However, predicting the magnitude and direction of herbivore impacts within and across systems remains challenging, in large part because changes in large herbivore assemblages are occurring alongside other prominent forms of human disturbance (e.g. climate change, species invasions). Synergies among these global change drivers complicate our understanding of plant–herbivore interactions, and it is now clear that the impacts of top-down forces are highly context dependent. One current theory predicts that herbivores enhance plant biodiversity at high productivity, but have the opposite effect at low productivity, due to observations of herbivore impacts varying strongly with abiotic site characteristics and underlying productivity (Augustine & McNaughton, 2006; Bakker et al., 2006; Borer et al., 2014; Sitters et al., 2020; Stahlheber & Antonio, 2013). Changes to global climate regimes are altering precipitation, air temperature and productivity patterns, resulting in a predicted decline in global ANPP (annual net primary productivity; Boone et al., 2018). Therefore, developing a better understanding of the role of climatic conditions in modulating herbivory effects will be increasingly important (Milchunas & Lauenroth, 1993; Osem et al., 2002; Proulx & Mazumder, 1998).

Yet, empirical support for the importance of site productivity as a mediator of herbivore impacts on plant communities is equivocal, with many deviations from the proposed pattern. This has led to the development of an alternative hypothesis: herbivore impacts on plant community richness and diversity are modulated by their impacts on plant species dominance, completely independent of site-level productivity or climatic conditions (Koerner et al., 2018). In this case, species invasions, nitrogen deposition and other global change factors that influence species dominance may have stronger effects on plant–herbivore interactions and plant diversity outcomes than productivity or climate, and the change in species dominance that can occur along abiotic gradients (Bowker et al., 2010; Menezes et al., 2020; Spasojevic & Suding, 2012) is ultimately responsible for the appearance of productivity or climate as a mediator of herbivore impacts.

Because competitive relationships among plants depend on resource availability (such as light and water; Inouye & Tilman, 1988; Kadmon, 1995; Tilman, 1982), herbivores should increase plant diversity when their effects alleviate plant competitive exclusion and constraints on species establishment (Eskelinen & Virtanen, 2005; Grubb, 1977; Knapp et al., 1999). The productivity–richness hypothesis suggests this may be especially important under wetter climatic conditions, where primary productivity is relatively high and large herbivores can prevent light competition by tall, dominant plant species (Bakker et al., 2006; Huisman et al., 1999; Huisman & Olff, 1998), and where increased light availability leads to enhanced germination and seedling establishment (Jutila & Grace, 2002; Koerner et al., 2018). Conversely, herbivores should decrease diversity under arid, low-productivity conditions, where nutrients and/or water are often limiting, plants are less resilient to grazing and trampling, and competition for space and light is more minimal (Inouye & Tilman, 1988). Here, herbivory may reduce species richness directly through preferential consumption of nutritious species, or indirectly by increasing resource limitation, stress or the abundance of a few herbivory-tolerant species (Berendse et al., 1992; Milchunas et al., 1988). In contrast, the dominance–richness hypothesis posits that it is solely herbivore-induced changes in the competitive environment that determine the response of plant biodiversity, irrespective of primary productivity. Under this hypothesis, when herbivores reduce the abundance (biomass and cover) of dominant species (e.g. because the dominant plant is palatable), additional resources become available to support new species, thereby increasing biodiversity.

Further examination of these hypotheses to better understand how competitive dynamics drive shifts in richness and diversity may be aided by field-based experiments conducted at appropriate scales. For instance, many experiments attempt to create homogeneous environments through a large number of small-scale exclosures across a patchwork of land use contexts. While deeply insightful in many ways, these may not represent the array of niche opportunities available to plant communities in real systems, which allow species to exploit resources more completely (Cardinale, 2011; Dimitrakopoulos & Schmid, 2004). Investigating these theories using larger scale experiments that incorporate both wild and domestic herbivores and encompass a range of microscale site variation within a single controlled experiment can advance our understanding of plant–herbivore relationships in the Anthropocene.

Here, we present the results of a large-scale, replicated field experiment (the Tejon Ranch Exclosure Experiment, TREE) which we initiated to directly compare the consequences of realistic large herbivore change scenarios—through wildlife loss and livestock addition—on vegetation structure and community diversity in an oak savanna system of high conservation value in southcentral California, USA. Critically, our study design enables us to experimentally investigate these two contrasting hypotheses in a tightly controlled experimental design conducted on a single parcel of land with uniform herbivore management and land use history. Our experiment uses a naturally occurring topoclimatic gradient to allow direct exploration of interactions among herbivores and aridity. Aridity is an abiotic factor highly correlated with productivity in our study area (Supplementary Materials), as it is in grassland and savanna ecosystems in general (Delgado-Baquerizo et al., 2013; Hufkens et al., 2016). California's oak savannas are a suitable location for this experiment because (a) they are experiencing rapid concomitant changes in ungulate assemblages and climate and (b) they have been the focus of extensive climate change experiments and modelling (e.g. Bartolome et al., 2007; Davis et al., 2019; Dudney et al., 2017; Zhu et al., 2016). Therefore, using this as a model system for investigating the modulators of herbivore impacts on plant communities can yield tremendous insight into whether/how changes in both top-down (herbivory) and bottom-up (aridity) forces interactively control plant community structure, and help predict changes likely to occur in the future.

Our study tests three fundamental research questions: (a) How do two common types of realistic changes in large herbivore assemblages impact vegetation structure (cover, bare ground, shading, litter and standing biomass) and community diversity (richness, phylogenetic diversity, Shannon diversity and dominance)? (b) How does variation in climate (aridity), a form of environmental heterogeneity that is changing rapidly and globally, affect the relationship between herbivore shifts and vegetation responses? (c) Can the impacts of wild and domestic herbivore on plant species dominance explain plant diversity responses? We hypothesized (a) herbivores suppress cover, standing biomass and litter accumulation, decrease shading and increase bare ground and these impacts will be mediated by the type of herbivores present, with livestock additions resulting in higher overall grazing pressure, resulting in stronger effects; (b) aridity differences across sites will result in a pattern of herbivores exerting stronger effects on structure at higher aridity; and (c) we expected that herbivores will enhance plant diversity where they have the greatest suppressive effects on cover and biomass, and/or where dominance is lowest and, conversely, suppress diversity where effects on structure are weak and/or where dominance is high; such that the greatest reduction in plant richness and diversity will occur when both wildlife and livestock are present under high aridity conditions, and stronger effects on structure will correspond with reduced dominance and increased richness and diversity.

2 | MATERIALS AND METHODS

2.1 | Study area

Tejon Ranch, located in the Tehachapi Mountains of southcentral California (34°59′N, 118°43′W), is a mixed cattle-ranch and wildlife conservation property, containing 97,124 ha of conserved lands that are jointly managed by the Tejon Ranch Company, Tejon Ranch Conservancy, and two grazing lessees. The ranch is uniquely positioned at the confluence of four of California's major ecoregions and is a region of high floristic conservation value. It also provides the only corridor for wildlife movement between the Angeles, Los Padres, and Sequoia National Forests and the southern Sierra Nevada. Dominant ungulate herbivores on the ranch include wild populations of mule deer *Odocoileus hemionus*, introduced Rocky Mountain elk *Cervus canadensis nelsoni*, pronghorn *Antilocapra americana* and invasive feral pig *Sus scrofa*, as well as an estimated 10,000 head of cattle *Bos taurus*. Cattle are moved seasonally from low elevation grasslands in the late fall through early spring, to higher elevations in the late spring through early fall, but are otherwise predominantly free ranging.

This area is characterized by rugged topography and steep aridity gradients, providing a suitable case study of local variation in climate and projected exposure to future climate change over the next century (McCullough et al., 2016). The regional climate is Mediterranean, with hot, dry summers and cooler, wetter winters. Mean annual precipitation for the period 1896–2010 varied from around 250 mm in the driest, low elevation portions of the ranch to over 500 mm at the highest elevations. At elevations above roughly 1,500–1,600 m, precipitation regimes are historically snow dominated (Western Regional Climate Center, 2015). Soils are fertile loamy residuum derived from igneous and metamorphic parent material and are classified as thermic type (low elevation) and mesic type (higher elevations) Haploxerolls according to US Soil Taxonomy (https://casoilresource.lawr.ucdavis.edu/gmap). These soils support a landscape mosaic of grassland, oak savanna and mixed hardwood forest. The overstorey at the study area is primarily composed of three species of oak (*Quercus douglasii*, *Q. lobata* and *Q. kelloggii*), with *Q. douglasii* dominating hot, dry savanna foothill sites, and *Q. kelloggii* constrained to mesic montane woodlands and forests; ponderosa pine *Pinus ponderosa* and white fir *Abies concolor* are also present (<10% canopy cover) on north-facing slopes above 1,372 m.

2.2 | Exclosure experiment design

Our exclosure experiment is located at the site of prior research measuring and modelling microclimates (Davis & Sweet, 2012; McCullough et al., 2016). Utilizing pre-existing downscaled climate grids (Davis & Sweet, 2012; McCullough et al., 2016), we selected three locations ('levels') to roughly represent present, near future and far future climate scenarios, with each site separated by approximately 2°C average temperature and 200–300 mm annual (water year) climate water deficit (CWD) and spanning elevations from 580 to 1,650 m (Figure 2; more details in Appendix S1). At each of the three climatically distinct levels—Arid (580 m elevation), Intermediate (1,650 m, south-facing slope) and Mesic (1,650 m, north-facing slope)—we selected a large tract of oak savanna–woodland of similar vegetation with no signs of recent burning or other large-scale disturbance and established three replicate randomized blocks (Figure 2). Each block contained three treatment levels of large herbivores—no-ungulates (total exclosure) which functionally excluded all large herbivores over 40 kg body mass with complete barriers, wild ungulates (partial exclosure) which used semi-permeable fencing to remove cattle, and wildlife + cattle (open, unfenced control; Figures 2a, 3).

Exclosures were completed in November 2016 and were 1 ha in size to capture community-wide responses. The experiment thus comprises a total of 27 1-ha plots: three plots/block, three blocks/level, three levels. Collectively, these treatments allowed the evaluation of the effects of large herbivore shifts that mimic changes occurring across western North America and worldwide (e.g. high

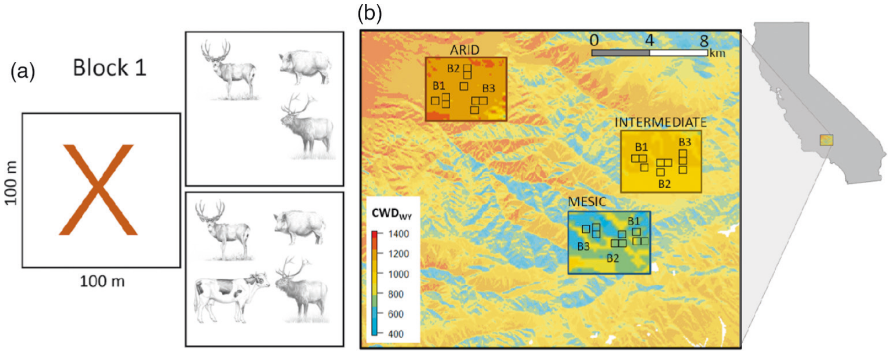

FIGURE 2 Schematic of an experimental block and map of the Tejon ranch Exclosure experiment (TREE). (a) the experiment utilizes nine blocks; each block consists of three treatment types: Open, unfenced plots accessible to all herbivores; partial exclosure plots that use semi-permeable fencing to exclude non-jumping herbivores (primarily cattle) and total exclosures that remove all adult large herbivores. Each plot is 1 ha in size (100 m × 100 m). (b) the nine blocks are clustered across three aridity levels (arid, intermediate and Mesic), selected based on downscaled models of climate water deficit (CWD). Mesic and intermediate blocks encompass montane oak savanna–woodland on north-facing and south-facing slopes, respectively. Arid blocks are situated in foothill savanna and have minimal slope

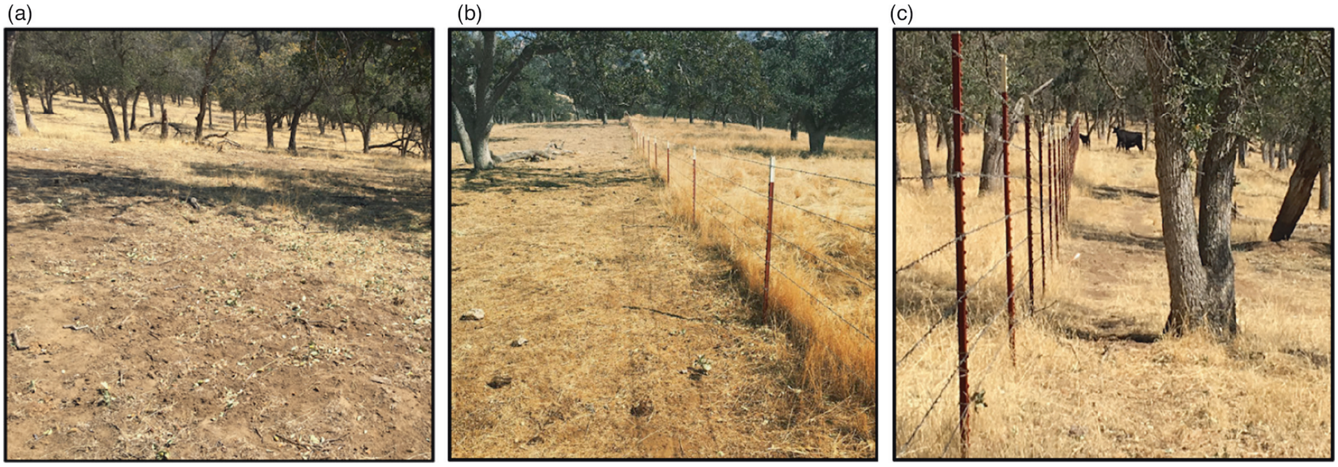

FIGURE 3 Photographs of open controls (a), partial exclosures (b) and total exclosures (c), in September at one block in the arid climate level at Tejon ranch, Kern co., CA. There is a visible increase in standing biomass inside partial and total exclosures in comparison to unfenced areas

densities with both wildlife and cattle, low to moderate density with no cattle and the presence of non-native wild ungulates, and extremely low densities simulating complete wildlife loss/removal). We note that, because all plots with similar climatic conditions are clustered together spatially to obtain replication while minimizing unintended sources of variation (Figure 2b), this design cannot fully distinguish between site and climatic effects. To help account for this, we examined variation in site characteristics such as plant composition, tree cover and soils, and found differences across sites are predominantly linked with climate variation, suggesting that this design issue is of minimal concern (for an evaluation of site-level conditions, see Appendix S2).

2.2.1 | Herbivore activity and exclosure efficacy

In each plot, we measured dung densities of wild ungulates and cattle along three 100 m × 4 m belt transects each spring (April–June), summer (July–September), fall (October–November) and winter (December–March), from 2017 to 2018. An observer walked each transect, counting each discrete dung pile and identifying species of origin. We calculated dung densities to ensure the effectiveness of experimental barriers (i.e. that target species were present and non-target species were absent), and to look for variation in activity levels of different herbivores across the three sites on the aridity gradient. Methods for analyses are detailed in Appendix S3.

2.2.2 | Investigating herbivore × aridity effects on plant communities

We focused on plant community responses that have been associated with downstream changes in ecosystem function, including (a) vegetation structural characteristics and (b) biodiversity. Structural characteristics included total vegetation cover, bare ground, late-season standing biomass (residual dry matter, RDM), spring remnant litter volume and shading. Total cover and litter volume serve as non-destructive proxies for biomass during the peak growing season (to minimize disturbance events within the plots, we aimed to limit the amount of destructive sampling to once per year). In California annual grasslands and savannas, RDM is a commonly used estimate of litter accumulation going into the growing season (Bartolome et al., 2007), while remnant litter volume is a measure of how much litter remains during the growing season peak after winter decomposition. We also investigated shading by measuring the change in photosynthetically active radiation (ΔPAR) from above to below understorey vegetation (HilleRisLambers et al., 2010).

We used multiple metrics to evaluate complementary aspects of biodiversity: species richness, Shannon Diversity, Berger–Parker dominance and phylogenetic diversity (measured as mean pairwise distance, MPD). Because there are a large number of exotic species in our system, particularly at Arid plots, we also investigated species richness and Shannon Diversity for exotic species independently (details can be found in Appendix S5). Each of these metrics provides unique insight into the community (though they can be correlated (Venail et al., 2015); see Appendix S6). Metrics were calculated in R (v 3.5.0, R Core Team, 2018). Richness and Shannon diversity were calculated with the VEGAN package (Oksanen et al., 2016): richness demonstrates taxonomic differences across communities, while Shannon diversity incorporates information on species evenness. Berger–Parker dominance demonstrates whether changes were due primarily to altered abundance of one dominant species and whether site-level dominance mediated herbivore effects; this was calculated as the relative abundance of the most abundant species per plot. Phylogenetic diversity was calculated as mean pairwise distance (MPD; Tucker et al., 2017) to account for evolutionary history. We constructed phylogenetic trees using Phylomatic (Webb & Donoghue, 2005) based on the APG III (2009) phylogeny, and calculated MPD for each community using the PICANTE package (Kembel et al., 2010; additional details in Appendix S4).

2.3 | Sampling design

We surveyed plots in 2019, 3 years after treatments were applied in 2016; this is a timeframe established by previous studies as suitable for detecting non-transient effects of herbivore removal (Borer et al., 2014; Jia et al., 2018; Koerner et al., 2018). The exception is for RDM, which was collected in fall 2018 (as it was material remaining at the end of 2018 that influenced growing conditions for the 2019 season). We surveyed species composition within 2 weeks of estimated peak NDVI at each site (USGS eModis), which resulted in surveys conducted in mid-April (Arid), mid-May (Intermediate) and mid-June (Mesic). Six 50 m survey transects were sampled in a grid in the central 0.25 ha of each 1 ha plot (similar in design to Goheen et al., 2013), and visually estimated species cover in 1 × 1 m subplots spaced every 10 m along transects ($n = 36$ per plot). At each subplot, we recorded total vegetation cover (up to 100%; distinct from cumulative cover which includes aerial overlap and therefore would exceed 100%), litter volume (area of 1 × 1 m subplot covered by litter multiplied by the average litter depth in that subplot)—bare ground (up to 100%), and species cover for each species rooted within the subplot (the sum of cumulative cover by all species could therefore exceed 100% owing to canopy overlap). The same observers conducted cover estimates for all species, and identified plants to species (or to genus for <5% of observations) using the Jepson Manual, the standard for California flora (Baldwin et al., 2012).

We evaluated shading by measuring the difference between photosynthetically active radiation (ΔPAR) above and below understorey vegetation in 10 locations (random selection of 10 of the 36 plant composition subplots) in each plot using a handheld quantum photometer (Apogee Instruments MQ-200). These measurements were made on consecutive cloudless days between 11:00 a.m. and 2:00 p.m., at peak biomass. We use ΔPAR to determine the percent of light reaching the soil surface as a proxy for competitive pressure for light. Light limitation has previously been attributed to species dominance and greater competition in terrestrial plant communities (e.g. Banta et al., 2008; Harpole & Tilman, 2006; Tilman et al., 2004; Violle et al., 2009; Vojtech et al., 2007; Wedin & Tilman, 1993). We expect this to be most relevant at low aridity, as water is expected to be the most limiting factor under arid conditions.

We harvested residual dry matter (RDM) in September–October (before the beginning of winter rains) by clipping five 0.25 × 0.25 m subplots within each plot, drying the biomass (60°C for 72 h), and weighing it.

2.4 | Statistical analyses

We tested the relationship between climate, herbivore treatment and vegetation response using linear mixed-effects models (LMMs). We included exclosure treatment ($n = 3$), aridity level ($n = 3$) and the interaction between aridity level and exclosure treatment as explanatory variables, and block ($n = 9$) as a random effect (Zuur et al., 2009). We fit all models using the LME4 package (Bates et al., 2015). We used this approach for each of the structural and diversity response variables described above. For each response, we selected the best fitting model by minimizing AICc values (MuMIn package, (Bartón, 2018), and generated *p*-values of the final models using parametric bootstrapping with 10,000 iterations (PBKRTEST package v 0.4–7, Halekoh & Højsgaard, 2014). We verified that model assumptions were met using the DHARMa package (version 0.2.0; Hartig, 2018). When a fixed effect with more than two levels was statistically significant ($p < 0.05$), we changed the level set as the baseline and re-ran the model to examine pairwise differences. To summarize the explanatory power of final models, we calculated the marginal (hereafter 'R^2_m') and conditional (hereafter 'R^2_c') coefficients of determination using the MuMIn package (Bartón, 2018). For each response variable, we used plot-wide means as a conservative unit of analysis. Descriptive statistics are reported as means and standard deviation unless otherwise specified.

3 | RESULTS

3.1 | Herbivore activity and exclosure efficacy

Monitoring of dung densities across the plots confirmed the efficacy of these treatments (Figure 4; see S3 for details). Surveys of dung in the exclosures showed that adults of numerically dominant, large herbivores which were abundant in the adjacent open access areas were successfully excluded by the total exclosures the majority of the time (Figure 4). Partial exclosures were successful at excluding cattle (Figure 4b). Feral pig dung was relatively low along transects, but signs of rooting and tracks were evident across all levels, and within some partial exclosure and open plots at Arid and Intermediate. Wildlife were less active within partial exclosures at Arid, and pigs were less active within partial exclosures across all climate levels, suggesting either an unintentional fence effect or a preference for foraging in locations also grazed by cattle (Appendix S3). Higher activity by wildlife in open plots may compound differences among open and partial treatments. Dung of omnivores and carnivores, which may have impacted ungulate behaviour, was not encountered frequently enough for meaningful statistical analysis, though we did observe signs (scat, prints, in-person sightings) of mountain lions in the immediate vicinity of most blocks, including within partial and total exclosure plots.

3.2 | Impact of herbivore exclusion and climate on vegetation structure

Herbivores had significant effects on the five structural metrics we examined. Control plots open to wildlife and cattle had reduced vegetation cover, litter, shading and RDM relative to partial and total exclosures (Figure 5). The weakest impacts were on total cover (Figure 5a); this may differed had we measured cover at the end (rather than the peak) of the growing season. Structural responses

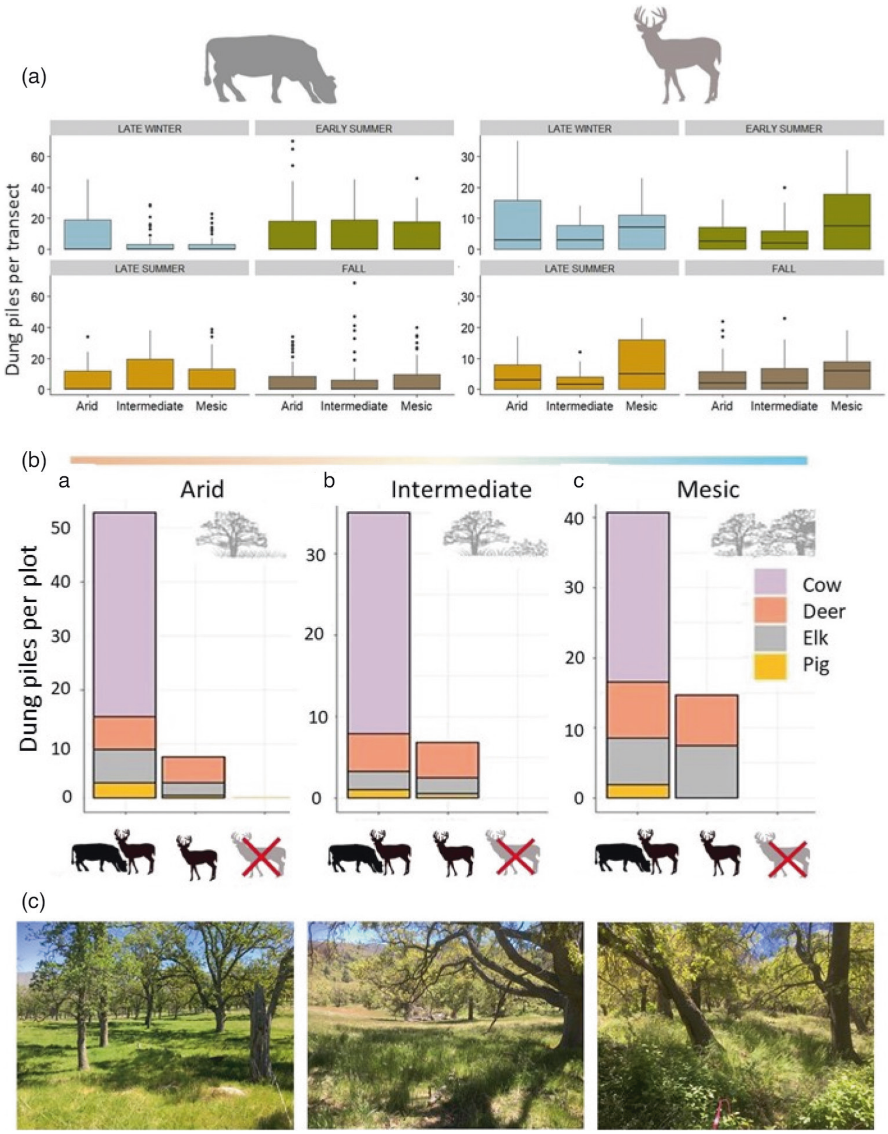

FIGURE 4 Counts of herbivore dung, a proxy for herbivore abundance, document activity patterns across experimental sites and seasons. (a) Box plots of activity patterns of large herbivores across seasons and aridity levels, showing median (middle line), upper and lower quartiles (top and bottom of box), and upper extremes (dots above box). Late winter counts in blue, early summer in green, late summer in tan and fall in brown. (b) Overall patterns in ungulate dung density across the three treatments and aridity levels show that cattle are additive to wildlife, with cattle in purple, deer in red, elk in grey and feral pig in yellow. Stacked bar graphs show mean values for each species; error bars have been omitted for visual clarity. (c) Photos of open plots across the three aridity levels (from left to right: Arid, intermediate, Mesic)

diverged between plots with both wildlife and cattle, and plots with wildlife only (Figure 5; Table 1). The independent effects of wildlife on vegetation structure were weak or undetectable, relative to the effects of wildlife and cattle combined.

Plant cover was slightly reduced in plots open to herbivory by wildlife and cattle relative to those with wildlife alone (partial exclosures) and total ungulate exclusion at both Arid and Mesic, but not Intermediate (Table 1; Figure 5). Herbivore treatment and aridity level were significant predictors of cover, and the best fit model also included the interaction of level and treatment (Table 1; Figure 5; $R^2_m = 0.50$, $R^2_c = 0.62$). Bare ground was higher in open plots at Arid and Intermediate than in partial or total exclosures, but not Mesic (Figure 5). Wildlife alone had no significant effect on bare ground (Figure 5). The best fit model for bare ground included herbivore treatment, aridity level and their interaction, though treatment was the only significant predictor (Table 1; Figure 5; $R^2_m = 0.36$, $R^2_c = 0.46$).

Litter volume increased significantly inside both partial and total exclosures across all aridity levels, though at Intermediate the difference between open and partial exclosures was not significant. Treatment and aridity were significant predictors; the best fit model included treatment, aridity level and their interaction (Table 1, Figure 5; $R^2_m = 0.84$, $R^2_c = 0.87$). Wildlife and cattle also substantially decreased shading (ΔPAR) relative to partial and total exclosures across all aridity levels, while there was no difference between partial and total exclosures (Table 1; Figure 5d; $R^2_m = 0.87$, $R^2_c = 0.87$). In other words, excluding herbivores increased shading by the understorey vegetation regardless of the exclosure type (total or partial) or aridity level. RDM also increased inside exclosures relative to open plots across all three aridity levels; the final LMM of RDM included herbivore treatment, aridity level and their interaction (Table 1; Figure 5e; $R^2_m = 0.93$; $R^2_c = 0.95$).

3.3 | Impact of herbivore exclusion on richness and diversity

Species richness and diversity diverged significantly across herbivore treatments, and these responses were modulated by aridity (Table 1;

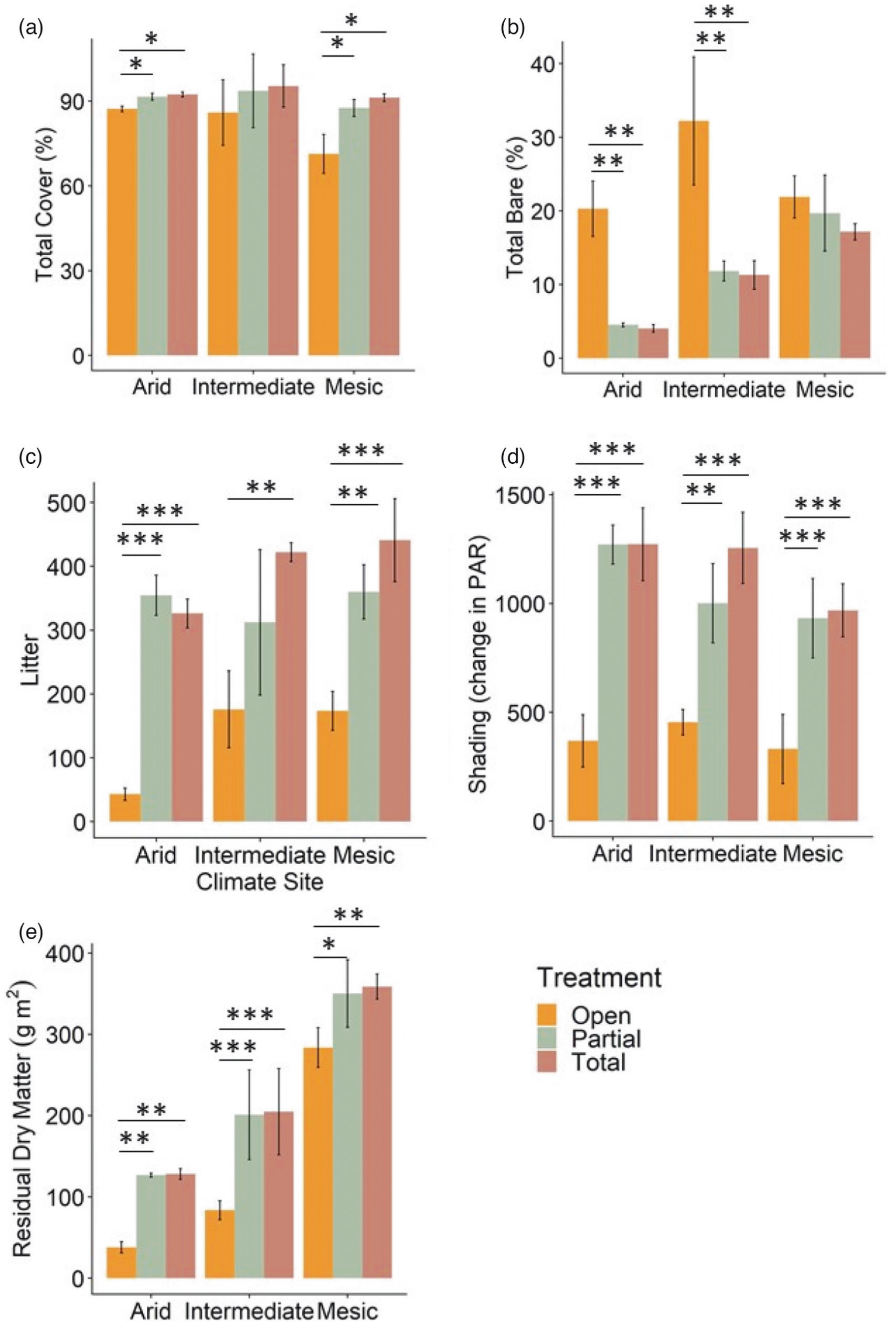

FIGURE 5 Bar graphs (means, ±*SD*) illustrating changes in structural metrics across treatments and climate levels. Asterisks indicate significant within-level differences among treatments (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$)

Figure 6a). Across all aridity levels, wildlife had a neutral to positive effect on richness (Figure 6a), while cattle with wildlife suppressed richness at Mesic and enhanced it at Arid (Table 1; Figure 6a). At Intermediate, herbivores had no effect on richness. The final LMM for species richness included terms for herbivore treatment, level and the interaction between treatment and climate level (Table 1; Figure 5; $R^2_m = 0.79$, $R^2_c = 0.88$).

At Arid, total herbivore exclusion decreased Shannon diversity relative to open control plots and partial exclosures (Figure 6b). There was no difference in Shannon diversity among treatments at Intermediate or Mesic. The final LMM for Shannon diversity included terms for herbivore treatment and the interaction between treatment and climate level (Table 1; Figure 6; $R^2_m = 0.73$, $R^2_c = 0.75$).

Treatment effects on MPD were somewhat stronger. At arid, MPD was greatest in open control plots, significantly lower in partial exclosures, and lowest in total exclosures. At intermediate, MPD was higher in open plots than partial exclosures, but there was no difference between partial and total exclosures or between open plots and total exclosures. There was no difference among treatments in MPD at Mesic. Similar to other diversity responses, the final model structure for MPD included treatment, aridity level and their interaction (Table 1; Figure 6; $R^2_m = 0.76$, $R^2_c = 0.76$).

When we examined effects on exotic species only, exotic Shannon diversity was highest in plots open to livestock and lowest in total exclosures; plots accessible only to wildlife had intermediate diversity at Arid and Mesic, but no significant difference

TABLE 1 Linear mixed model results for the effects of herbivore treatments (open, partial exclusion and total exclusion) and site aridity on plant structure and diversity metrics (degrees of freedom = 2,18 for treatment; 2,18 for site; and 4,18 for treatment × site). Models include block nested within aridity level as a random effect. Bold values indicate a statistically significant difference

	Herbivore treatment		Aridity level		Treatment × level	
Response	*F*-value	*p*-value	*F*-value	*p*-value	*F*-value	*p*-value
Structural metrics						
Total cover	**9.49**	**0.002**	**5.04**	**0.020**	1.39	0.281
Litter volume	**62.82**	**<0.001**	**5.99**	**0.010**	2.45	0.084
Bare Substrate	**4.81**	**0.023**	2.38	0.124	0.71	0.595
RDM	**37.03**	**<0.001**	**184.75**	**<0.001**	0.87	0.502
ΔPAR	**78.17**	**<0.001**	**5.85**	**0.011**	1.77	0.180
Diversity metrics						
Richness	**6.52**	**0.012**	**17.89**	**0.003**	**10.20**	**0.001**
Shannon	**6.58**	**0.012**	**11.28**	**0.009**	**8.28**	**0.002**
Berger–Parker	**5.99**	**0.010**	**12.32**	**<0.001**	**4.53**	**0.010**
MPD	**16.91**	**<0.001**	**6.81**	**0.006**	**8.80**	**<0.001**

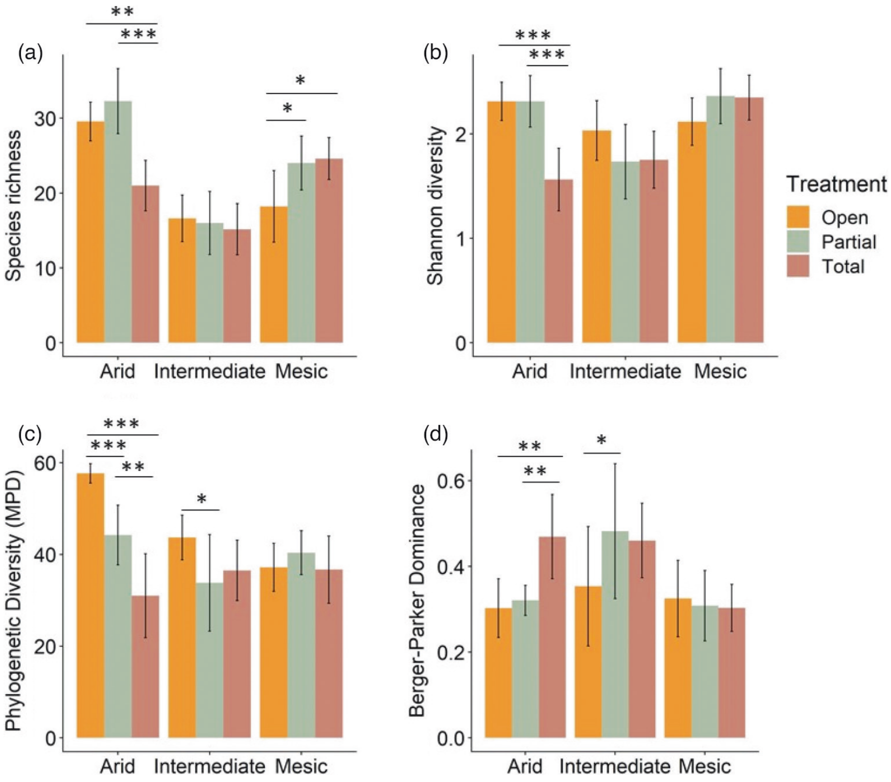

FIGURE 6 Bar graphs (means, ±*SD*) of herbivore effects on (a) species richness, (b) Shannon diversity, (c) phylogenetic diversity (mean pairwise distance) and (d) Berger–Parker dominance. Asterisk indicates significant within-level differences among treatments (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$)

at Intermediate. Exotic species richness was significantly different across all three herbivore treatments at Arid, with again highest richness at open plots, but was not significantly different across treatments at Intermediate or Mesic (where overall abundance was lower than at Arid; details in Appendix S4).

3.4 | Herbivore exclusion effects on dominance

Similar to diversity responses, dominance responses were stronger under arid conditions (Figure 6). Dominance was significantly higher within total exclosures at Arid relative to open controls and partial exclosures. At Intermediate, dominance increased in partial exclosures relative to open plots (the inverse of treatment effects on MPD). Treatment had no significant effect on MPD at Mesic. The final LMM for dominance included terms for herbivore treatment, level, and the interaction between treatment and level (Table 1; Figure 6; $R^2_m = 0.68$; $R^2_c = 0.68$).

4 | DISCUSSION

We found that the removal of large herbivores impacted both vegetation structure and plant community diversity. Climatic context modulated the combined effects of wildlife and cattle on plant richness and diversity, while effects on structure were generally consistent across the three climatic contexts we examined. Our results support previous work in demonstrating that plant communities are shaped by interactions among top-down (herbivory) and bottom-up (climatic context) forces, and we show that changes to both herbivore abundances and climatic conditions can synergistically drive plant community change. However, the effects of livestock and wildlife together differed substantially from the effects of wildlife alone, indicating the functional consequences of realistic changes in large herbivore assemblages—either through the addition of cattle or wildlife loss and replacement by cattle—may differ from the consequences of wildlife or wildlife loss in isolation.

4.1 | Effects of herbivores on plant communities across the climate gradient

Consistent with other observations and experiments (Bakker et al., 2006; Young et al., 2013; Burkepile et al., 2017), we found ungulate herbivores had strong impacts on plant structure and community diversity. Sites open to wildlife and cattle had reduced vegetation cover, RDM, litter and shading. In the presence of cattle and wildlife, RDM, litter and shading were lower in arid than in mesic contexts, while herbivores also increased bare ground at Arid and Intermediate, but had no significant impact at Mesic (Figure 5). These structural responses were most notable for plots with both wildlife and cattle (Figure 5; Table 1). The independent effects of wildlife on vegetation structure were more likely to be weak or undetectable, relative to the effects of wildlife and cattle combined. Arid blocks (the most arid of our three topoclimatic sites) were located near the transition zone from savanna to grassland, and Mesic blocks (the least arid of our sites) were set on the ecotone from savanna to mixed hardwood forest so that our experiment very nearly encompassed the full climatic range of oak savanna–woodlands in this region. Notably, we did not see consistently stronger effects of herbivory on vegetation structure under high aridity, as has been observed in other systems (e.g. Goheen et al., 2013; Young et al., 2013). In contrast, when both livestock and wildlife are present, we find effects on litter accumulation, shading and RDM appear to be similar at all climates in this oak savanna system.

Richness and diversity also diverged strongly across herbivore treatments (open vs. partial), and these responses were strongly modulated by aridity. We originally hypothesized that if the productivity–richness theory was supported, climatic conditions should drive variation in magnitude and direction of plant community response to herbivores (Bakker et al., 2006; Milchunas & Lauenroth, 1993; Olff & Ritchie, 1998), with stronger positive effects of herbivores on diversity when environmental stress was low (i.e. lower temperature, higher moisture, higher productivity environments), and stronger negative effects when environmental stress was high (Bakker et al., 2006). However, what we observed was that the presence of cattle inverted the effect of herbivores on plant diversity along the climate gradient to opposite what would be expected based on this theory. While wild ungulates always had a neutral or positive effect on diversity across all three aridity levels, wildlife with livestock had neutral (for dominance, MPD and Shannon diversity) to negative effect (for richness) at low aridity, and a strong positive effect on richness and diversity (and a strong negative effect on dominance) at high aridity. These results demonstrate a pattern opposite that from other exclusion experiments at local, topographically determined gradients (Osem et al., 2002; Osem et al., 2004) as well as from gradients at regional (Frank & Esper, 2005; Young et al., 2013), continental (Lezama et al., 2014) and intercontinental scales (Bakker et al., 2006; Milchunas & Lauenroth, 1993).

4.2 | Effect of livestock presence on plant responses: Importance of density, species identity and foraging strategy

Our results demonstrate that the changes in plant communities in response to declines of wild herbivores in experimental sites do not closely approximate the changes that occur in plant communities in more typical landscapes in which livestock have joined (or replaced) wildlife. There are a number of possible reasons cattle presence may lead to different effects on plant communities. First, because domestic livestock are typically stocked at higher densities than those at which wild large herbivores naturally occur, the addition of livestock creates higher overall herbivory pressure through increased total density (Barnosky, 2008; Prins et al., 1992). The classic grazing curve suggests that intermediate levels of herbivory should result in the highest species richness (intermediate disturbance hypothesis), with richness lowest at the two grazing extremes (Grime, 1973). This hump-shaped grazing curve has been documented in many grassland ecosystems (Mwendera et al., 1997; Olff & Ritchie, 1998; Suominen et al., 2003). In our experiment, the relatively lower levels of disturbance generated by wild ungulates may have a marginal to modest beneficial effect on diversity by preventing competitive exclusion and providing a marginal release of constraints on plant establishment. Meanwhile, the disturbance created by relatively higher densities of livestock may push this interaction from facilitative to antagonistic, if plant species are unable to recover from higher levels of grazing and trampling. Future experiments that consider an array of livestock densities across resource gradients would help separate the effect of density independent of identity, and identify whether or when such density thresholds exist.

In respect to identity, differences in foraging strategies among different guilds may also be an important factor, producing contrasting effects on both spatial and temporal heterogeneity in vegetation structure and composition (Adler & Lauenroth, 2000; McNaughton, 1984). A key difference between wild herbivores and cattle is that the deer and elk present in this system are mixed feeders, typically also feeding substantially on woody species. Therefore, differences in foraging preferences among cattle, elk, deer and pig may play an important role in our study system, particularly at Intermediate and Mesic sites where woody shrub cover is higher. Cattle consumption of dominant grass species at Arid and to a lesser degree, Intermediate, contrasts sharply with their avoidance of the thorny shrub which is the dominant cover type at Mesic (though they do still substantially impact shrub cover by physical destruction and trampling when looking for forage). This difference can largely explain the positive effect of livestock on plant diversity at Arid (e.g. where the dominant plant species is palatable), and negative effect at Mesic (where the dominant plant species is *not* palatable). Meanwhile, wild herbivores which are grazing relatively infrequently as well as browsing on woody species, maintain a relatively consistent neutral to positive effect across all climatic contexts.

Differences in the timing, duration and frequency of grazing, as well as the degree of selectivity, among wild and domestic herbivores may have different physiological and demographic consequences for the herbaceous plant species they consume. Facilitative interactions among cattle and wildlife have also been reported (Augustine et al., 2011; Odadi et al., 2011), and the high degree of diet overlap between elk and mule deer in the spring and cattle in the winter in the western U.S. indicates wildlife may preferentially use sites that have been previously grazed by livestock (Berg & Hudson, 1982; Kasworm et al., 1984). Ultimately, identity and density shifts are likely both extremely important, and interactively create either more heterogeneous or more homogeneous plant communities depending on palatability of the species present and feeding preferences of the species consumers present.

Unfortunately, we are unable to parse which of these possible mechanisms is responsible for the patterns we observed due to limitations of our experimental design, but ultimately, we argue that distinguishing between density and identity effects, in this case, may not be a top priority given the two are occurring simultaneously in rangelands worldwide. Our results would likely not help to predict what would happen in a place where wildlife were to exponentially increase, but that was not the aim of this study. Rather, we demonstrate that in landscapes undergoing multiple common simultaneous changes—namely wildlife declines, the addition of cattle and increasing aridity—outcomes will differ from predictions generated through experiments that incorporate only one or two of these factors, and our results suggest that at realistic stocking densities, the presence of livestock can significantly alter the effects of wild herbivores alone across environmental gradients.

4.3 | Productivity–richness and dominance–richness relationships

Established theory on context dependency of herbivore impacts on plant richness and diversity (i.e. productivity–richness relationships, dominance–richness relationships, e.g. Koerner et al., 2018) is based on several assumptions about interspecific competitive dynamics among plant species. If any of those assumptions are not met, it follows that unexpected outcomes may be observed. For instance, in regard to productivity effects on richness, if below-ground dynamics under arid conditions are not more important than above-ground interactions, grazing may have a different effect than predicted. For dominance–richness relationships, if the dominant plant species at a site is not highly palatable, herbivores are more likely to reduce diversity (as discussed above).

Ultimately, the results of our experiment suggest that neither productivity alone nor dominance change alone can fully predict the effects of wild and domestic herbivores on plant communities. Plots open to livestock and wildlife had reduced dominance at Arid, lower dominance relative to partial exclosures at Intermediate and no change at Mesic (Figure 6). In support of the dominance–richness theory, richness was lower within total exclosure plots at Arid, and while there was no effect of herbivore treatments on richness at Intermediate. At Mesic, richness increased inside total exclosures with no parallel decline in dominance; however, MPD was higher at Intermediate in plots with lower dominance. While our results provide somewhat equivocal support for the dominance-richness hypothesis, we also observed some diversity responses that were inverted from those predicted by the productivity–richness theory. While climatic context strongly mediated herbivore impact, it appears that this likely occurred indirectly, through climate-driven changes in species composition, which, in turn, led to changes in dominant species with differing levels of palatability to cattle and wildlife across the aridity gradient. Both of these theories seek a predictive way to generalize herbivore impacts on plant biodiversity across systems, and while seemingly contradictory, at their core, both suggest that if the most abundant species at a given site is palatable to the dominant herbivore, herbivores will increase richness and diversity, and vice versa. Indeed, this also appears to be the key takeaway from our study.

4.4 | Further considerations

Like most systems in western North America which have been highly modified by human activities, Tejon Ranch, while of high conservation value, is far from pristine. The ranch has a history of sheep and cattle grazing dating back to the 1800s, which has lingering legacy effects (Browning & Archer, 2011; Cuddington, 2011). Like most of California's grasslands, low to mid-elevation grasslands on the ranch are highly invaded, dominated by exotic grasses including *Bromus diandrus*, *Bromus hordaceus* and *Bromus tectorum* (Appendix S4). *Bromus diandrus* in particular has been associated with declines in plant species richness (Molinari & D'Antonio, 2020). Dominance by these exotic grasses covaries with aridity at our sites (Appendix S4), so we are unable to decouple effects of invasion status from effects of aridity, but it would stand to reason that non-native species may exhibit different traits than species that evolved under the environmental stressors in our study region, which may result in the disruption of theorized competitive dynamics along the climate gradient. If this is the case, this would have broader relevance beyond Tejon, particularly in other Mediterranean-type grasslands that have high numbers of plant invaders (Gritti et al., 2006), and help explain why livestock presence was so strongly correlated with higher richness and diversity under arid conditions at our site. This is supported by our results that richness and diversity of exotic species increased in the presence of livestock and wildlife across climatic contexts in our study. Based both on our results and numerous prior studies, plant invasion status may be important to consider in future work.

Alternatively, we assumed that higher stress is correlated with higher aridity, which may be incorrect. Somewhat counterintuitively, it may be that at lower aridity, the increased amelioration of heat and water stress due to increased standing biomass and resulting increases in shading (similar to conclusions drawn by Burkepile & Parker, 2017) may actually be more important because these communities did not evolve under severe water limitation, and may therefore be more vulnerable to moisture loss. This would align with other work in this system indicating that high elevations are more threatened by continued climate change than lower elevation, more arid communities, as historically energy-limited locations are becoming increasingly moisture limited (McCullough et al., 2016). Further investigation of light and water constraints would elucidate how large herbivores and topoclimates interact to generate heterogeneous hydrologic conditions in space and over time, supporting different spatial patterns of plant richness and diversity. This would assist in identifying when livestock and wildlife grazing will promote diversity and when it will suppress it, an important step for plant biodiversity conservation, particularly in this floristic biodiversity hotspot (Myers et al., 2000).

Finally, it is also possible that the diversity patterns we observed when cattle were present were partly attributable to subsequent changes in interspecific plant interactions. For instance, *Ericameria* and *Ribes*, two genera of woody shrub found at Intermediate and Mesic aridity levels, can both serve as nurse plants, sheltering palatable herbaceous species from herbivory (Milchunas & Noy-Meir, 2002; personal observation). This may explain the increased richness within exclosures at Mesic that we observed. Shrubs such as *Ericameria* spp. have been shown to increase beta diversity and alter species richness patterns (Kleinhesselink et al., 2014). Given that such plant–plant interactions may further mediate responses to herbivores (Richter, 2015), integrating interactions among functional groups into future studies to more mechanistically predict the response of plants to herbivores across climate gradients may be a fruitful avenue of investigation.

4.5 | What do herbivore assemblage shifts mean for the future?

Results from exclosure experiments are likely to best represent plant community responses where wildlife declines are the primary form of disturbance, for example, in protected areas (Craigie et al., 2010). However, given that protected areas form just under 15% of Earth's land area (IUCN *2016 Protected Planet* report) and not all protected areas exclude livestock grazing (i.e. Soofi et al., 2018), while rangeland occupies 30%–40% of Earth's land area (Asner et al., 2004), we must consider effects of livestock addition alongside changes in abundance of wildlife populations. Particularly in western North America, where ranching has become an important cultural legacy over the last two centuries, wildlife will need to coexist with increasing densities of humans and livestock, necessitating the consideration changes in livestock abundance in tandem with wildlife declines. Our results suggest that livestock effects can change both the magnitude and direction of many plant responses and alter the interaction with climate.

The climate variation across our experiment, which serves as a rough space-for-time proxy for how climate change might alter plant–herbivore interactions in oak savannas, suggests critical interactions will change in the future. Specifically, our results show that as these systems become hotter and drier, the reduction or elimination of livestock grazing would result in the loss of diversity at the drier extents of oak savannas (at least in exotic-dominated areas) while increasing diversity in the more mesic parts of this ecosystem. In the near future, effects of ungulate herbivore on diversity are attenuated. Forecasting into the future, as blue and valley oak savannas are expected to experience substantial range contractions (Kueppers et al., 2005; Sork et al., 2010), herbivory by livestock and wildlife may become an increasingly important factor for maintaining herbaceous plant biodiversity under further warming and drying.

5 | CONCLUSIONS

This study provides novel insight into how real-world stressors impact savanna plant structure and diversity. Our results indicate that large herbivore effects overpower climate effects for many vegetation responses linked to ecosystem function. This is an important finding because it suggests that in comparison to climate change—even mean temperature change exceeding 6°C—herbivore change can have a stronger impact on vegetation structure, and one of the main effects of climate change may be through its interaction with herbivores. Therefore, the two must be considered in conjunction if we want to manage for stable plant communities.

Furthermore, our results demonstrate that cattle do not elicit simple stepwise increases in all vegetation responses proportionate to their abundance. For diversity responses in particular, cattle can often cause the opposite effect that wild herbivores do, casting doubt on practices of using domestic herbivores to maintain diversity, particularly in more mesic systems. Whether this is due to density or some aspect of identity or management of livestock is an open question and should be investigated in future studies. Our results indicate that livestock and wildlife interact with climate in different ways, suggesting that even where livestock may be serving as useful proxies for lost wildlife under current climatic conditions, they may not be appropriate proxies in future climates.

This experiment was designed to help predict future patterns in human-dominated ecosystems, where novel combinations of species and abiotic contexts may lead to unexpected outcomes. While studying near-pristine systems that retain much of their late Pleistocene megafauna assemblages provides critical insight into how large herbivores have historically shaped plant communities and how these relationships have evolved, understanding how relationships between herbivores and plant communities may change in the future also requires investigation of real-world scenarios in which landscapes are heavily disturbed by multiple stressors. Our results support and extend the prior experiments that have considered context-dependent assemblage shifts through size-selective removals (Burkepile et al., 2017; Goheen et al., 2013; van der Plas et al., 2016; Young et al., 1997), and support the prior conclusion that grassland and savanna community structure responds more rapidly and strongly to ungulate herbivore removal in systems with less functional redundancy in ungulate communities, as noted in Koerner et al. (2014). Taken together, these prior experiments combined with ours provide a more complete understanding of ungulate herbivore controls on plant community structure in the past, present and future.

ACKNOWLEDGEMENTS

We thank Michael White, Mitchell Coleman, Tim and Susan Bulone, and all of the Tejon Ranch Conservancy for their collaboration and support. We thank the M2M project team (NSF award #1065864) for use of their climate data. We also greatly appreciate the plant identification assistance of Nick Jensen and Bruce Orr. This work would not have been possible without the field assistance of G. Najm, J. Murphy, J. Lin, A. Tokuryama and T. Ayers. Carla D'Antonio, Lauren Ponisio, Frank Davis, Heili Lowman and the Young Lab at UC Santa Barbara provided invaluable comments and discussions. We also thank Colin Jordan for his tremendous support. This work was supported by funding from the National Science Foundation (DEB award #1900502), the Hellman Foundation, the University of California Santa Barbara, the Sage and Sea Audubon Society, the Worster Family Foundation, and the UC Institute for the Study of Ecological and Evolutionary Climate Impacts. Funding for DAO was provided by the Department of Defence National Science and Engineering Graduate Research Fellowship. Any opinions, findings and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of funding agencies.

AUTHORS' CONTRIBUTIONS

D.A.O. and H.S.Y. conceived the ideas and designed the methodology; I.M.M. collected the climate data upon which this project was built and assisted with selection of the experiment's location; H.S.Y. and D.A.O. received the funding for this project; D.A.O., A.B., M.K., M.L., K.K., C.M. and I.M. collected the data; D.A.O. analysed the data; D.A.O. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.13871.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository https://doi.org/10.25349/D94W48 (Orr et al., 2022).

ORCID

Devyn A. Orr https://orcid.org/0000-0002-6899-5804
An Bui https://orcid.org/0000-0002-9548-7776
Maggie Klope https://orcid.org/0000-0003-3926-7039
Ian M. McCullough https://orcid.org/0000-0002-6832-674X
Hillary S. Young https://orcid.org/0000-0003-0449-8582

REFERENCES

Adler, P. B., & Lauenroth, W. K. (2000). Livestock exclusion increases the spatial heterogeneity of vegetation in Colorado shortgrass steppe. *Applied Vegetation Science*, *3*(2), 213–222. https://doi.org/10.2307/1479000

Asner, G. P., Elmore, A. J., Olander, L. P., Martin, R. E., & Harris, T. (2004). Grazing systems, ecosystem responses, and global change. *Annual Review of Environment and Resources*, *29*, 261–299. https://doi.org/10.1146/annurev.energy.29.062403.102142

Augustine, D. J., & McNaughton, S. J. (2006). Interactive effects of ungulate herbivores, soil fertility, and variable rainfall on ecosystem processes in a semi-arid savanna. *Ecosystems*, *9*(8), 1242–1256. https://doi.org/10.1007/s10021-005-0020-y

Augustine, D. J., Veblen, K. E., Goheen, J. R., Riginos, C., & Young, T. P. (2011). Pathways for positive cattle–wildlife interactions in semi-arid rangelands. *Smithsonian Contributions to Zoology*, *632*, 55–71. https://doi.org/10.5479/si.00810282.632.55

Bakker, E. S., Ritchie, M. E., & Olff, H. (2006). Herbivore impact on grassland diversity depends on habitat productivity and herbivore size herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. *Ecology Letters*, *9*, 780–788. https://doi.org/10.1111/j.1461-0248.2006.00925.x

Baldwin, B. G., Goldman, D. H., Keil, D. J., Patterson, R., & Rosatti, T. J. (2012). *The Jepson manual: Vascular plants of California*. University of California Press.

Banta, J. A., Stark, S. C., Stevens, M. H. H., Pendergast, T. H., IV, Baumert, A., & Carson, W. P. (2008). Light reduction predicts widespread patterns of dominance between asters and goldenrods. *Plant Ecology*, *199*(1), 65–67. https://doi.org/10.1007/s11258-008-9412-3

Barnosky, A. D. (2008). Megafauna biomass tradeoff as a driver of quaternary and future extinctions. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(Suppl 1), 11543–11548.

Bar-On, Y. M., Phillips, R., & Milo, R. (2018). The biomass distribution on earth. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(25), 6506–6511. https://doi.org/10.1073/pnas.1711842115

Bartolome, J. W., Barry, W. J., Griggs, T., & Hopkinson, P. (2007). Valley grassland. In M. Barbour, T. Keeler-Wolf, & A. A. Schoenherr (Eds.), *Terrestrial vegetation of California* (3rd ed., pp. 367–393). University of California Press. https://doi.org/10.1525/california/9780520249554.003.0014

Bartón, K. (2018). *MuMIn: Multi-model inference. R package version 1.42. 1*.

Bates, D., Kliegl, R., Vasishth, S., & Baayen, R. H. (2015). Parsimonious mixed models. *ArXiv Preprint ArXiv:1506.04967*.

Berendse, F., Elberse, W. T., & Geerts, R. (1992). Competition and nitrogen loss from plants in grassland ecosystems. *Ecology*, *73*(1), 46–53.

Berg, B. P., & Hudson, R. J. (1982). Elk, mule deer, and cattle: Functional interactions on foothills range in southwestern Albertafood, use of habitats. In *Proceedings of the wildlife-livestock relationships symposium: Held at Coeur d'Alene, Idaho, April 20–22, 1981/sponsored by Department of Wildlife Resources, University of Idaho; [James M. peek, PD Dalke, editors]*. Forest, Wildlife & Range Experiment Station, University of Idaho.

Boone, R. B., Herrero, M., Conant, R. T., Sircely, J., & Thornton, P. K. (2018). Climate change impacts on selected global rangeland ecosystem services. *Global Change Biology*, *24*(3), 1–12. https://doi.org/10.1111/gcb.13995

Borer, E. T., Seabloom, E. W., Gruner, D. S., & Harpole, W. S. (2014). Herbivores and nutrients control grassland plant diversity via light limitation. *Nature*, *508*(7497), 517–520. https://doi.org/10.1038/nature13144.Rights

Bowker, M. A., Soliveres, S., & Maestre, F. T. (2010). Competition increases with abiotic stress and regulates the diversity of biological soil crusts. *Journal of Ecology*, *98*(3), 551–560.

Browning, D. M., & Archer, S. R. (2011). Protection from livestock fails to deter shrub proliferation in a desert landscape with a history of heavy grazing. *Ecological Applications*, *21*(5), 1629–1642. https://doi.org/10.1890/10-0542.1

Burkepile, D. E., Fynn, R. W. S., Thompson, D. I., Lemoine, N. P., Koerner, S. E., Eby, S., … Smith, M. D. (2017). Herbivore size matters for productivity–richness relationships in African savannas. *Journal of Ecology*, *105*(3), 674–686. https://doi.org/10.1111/1365-2745.12714

Burkepile, D. E., & Parker, J. D. (2017). Recent advances in plant–herbivore interactions. *F1000Research*, *6*(119), 1–13. https://doi.org/10.12688/f1000research.10313.1

Cardinale, B. J. (2011). Biodiversity improves water quality through niche partitioning. *Nature*, *472*(7341), 86–89. https://doi.org/10.1038/nature09904

Charles, G. K., Porensky, L. M., Riginos, C., Veblen, K. E., & Young, T. P. (2017). Herbivore effects on productivity vary by guild: Cattle increase mean productivity while wildlife reduce variability. *Ecological Applications*, *27*(1), 143–155. https://doi.org/10.1002/eap.1422

Cleland, E. E., Lind, E. M., Decrappeo, N. M., Delorenze, E., Wilkins, R. A., Adler, P. B., … Seabloom, E. W. (2019). Belowground biomass response to nutrient enrichment depends on light limitation across globally distributed grasslands. *Ecosystems*, *22*, 1466–1477. https://doi.org/10.1007/s10021-019-00350-4

Collen, B., Loh, J., Whitmee, S., Rae, L. M. C., Amin, R., & Baillie, J. E. M. (2009). Monitoring change in vertebrate abundance: The living planet index. *Conservation Biology*, *23*(2), 317–327. https://doi.org/10.1111/j.1523-1739.2008.01117.x

Collins, S. L., Knapp, A. K., Briggs, J. M., Blair, J. M., & Steinauer, E. M. (1998). Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science*, *280*(May), 745–747.

Craigie, I. D., Baillie, J. E. M., Balmford, A., Carbone, C., Collen, B., Green, R. E., & Hutton, J. M. (2010). Large mammal population declines in Africa's protected areas. *Biological Conservation*, *143*(9), 2221–2228. https://doi.org/10.1016/j.biocon.2010.06.007

Crowther, T. W., Riggs, C., Lind, E. M., Borer, E. T., Seabloom, E. W., Hobbie, S. E., … Routh, D. (2019). Sensitivity of global soil carbon stocks to combined nutrient enrichment. *Ecology Letters*, *22*, 936–945. https://doi.org/10.1111/ele.13258

Cuddington, K. (2011). Legacy effects: The persistent impact of ecological interactions. *Biological Theory*, *6*(3), 203–210. https://doi.org/10.1007/s13752-012-0027-5

Davis, F. W., & Sweet, L. C. (2012). From mountain microclimates to the macroecology of tree species distributions in California. *Cirmount*, *6*, 2–5.

Davis, K. T., Dobrowski, S. Z., Higuera, P. E., Holden, Z. A., Veblen, T. T., Rother, M. T., … Maneta, M. P. (2019). Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(13), 6193–6198. https://doi.org/10.1073/pnas.1815107116

de Haan, C., Steinfeld, H., & Blackburn, H. (1997). *Livestock & the environment: Finding a balance*. European Commission, Directorate-General for the Environment.

Delgado-Baquerizo, M., Maestre, F. T., Gallardo, A., Bowker, M. A., Wallenstein, M. D., Quero, J. L., … Zaady, E. (2013). Decoupling of soil nutrient as a function of aridity in global drylands. *Nature*, *502*(7473), 672–676. https://doi.org/10.1038/nature12670

Dimitrakopoulos, P. G., & Schmid, B. (2004). Biodiversity effects increase linearly with biotope space. *Ecology Letters*, *7*, 574–583. https://doi.org/10.1111/j.1461-0248.2004.00607.x

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, *345*(6195), 401–406. https://doi.org/10.1126/science.1251817

Dudney, J., Hallett, L. M., Larios, L., Farrer, E. C., Erica, N., Stein, C., & Suding, K. N. (2017). Lagging behind: Have we overlooked previous-year rainfall effects in annual grasslands? *Journal of Ecology*, *105*, 484–495. https://doi.org/10.1111/1365-2745.12671

Eskelinen, A., & Virtanen, R. (2005). Local and regional processes in low-productive mountain plant communities: The roles of seed and microsite limitation in relation to grazing. *Oikos*, *110*(2), 360–368.

Fay, P. A., Prober, S. M., Harpole, W. S., Knops, J. M. H., Bakker, J. D., Borer, E. T., … Yang, L. H. (2015). Grassland productivity limited by multiple nutrients. *Nature Plants*, *1*(7), 1–5.

Firn, J., Nguyen, H., Schütz, M., & Risch, A. C. (2019). Leaf trait variability between and within subalpine grassland species differs depending on site conditions and herbivory. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1907), 20190429.

Forbes, E. S., Cushman, J. H., Young, T. P., Klope, M., & Young, H. S. (2019). Synthesizing the effects of large, wild herbivore exclusion on ecosystem function. *Functional Ecology*, *33*, 1597–1610. https://doi.org/10.1111/1365-2435.13376

Frank, D., & Esper, J. (2005). Characterization and climate response patterns of a high-elevation, multi-species tree-ring network in the European Alps. *Dendrochronologia*, *22*, 107–121. https://doi.org/10.1016/j.dendro.2005.02.004

Gao, J., & Carmel, Y. (2020). A global meta-analysis of grazing effects on plant richness. *Agriculture, Ecosystems & Environment*, *302*, 107072.

Goheen, J. R., Palmer, T. M., Charles, G. K., Helgen, K. M., Kinyua, S. N., Maclean, J. E., … Pringle, R. M. (2013). Piecewise disassembly of a large-herbivore community across a rainfall gradient: The UHURU experiment. *PLoS ONE*, *8*(2), e55192. https://doi.org/10.1371/journal.pone.0055192

Grime, J. P. (1973). Competitive exclusion in herbaceous vegetation. *Nature*, *242*, 344–347. https://doi.org/10.1038/246421a0

Gritti, E. S., Smith, B., & Sykes, M. T. (2006). Vulnerability of Mediterranean Basin ecosystems to climate change and invasion by exotic plant species. *Journal of Biogeography*, *33*, 145–157. https://doi.org/10.1111/j.1365-2699.2005.01377.x

Grubb, P. J. (1977). The maintenance of species-richness in plant communities: The importance of the regeneration niche. *Biological Reviews*, *52*(1), 107–145.

Halekoh, U., & Højsgaard, S. (2014). A Kenward-Roger approximation and parametric bootstrap methods for tests in linear mixed models – The R package pbkrtest. *Journal of Statistical Software*, *59*(9), 1–30.

Harpole, W. S., & Tilman, D. (2006). Non-neutral patterns of species abundance in grassland communities. *Ecology Letters*, *9*, 15–23. https://doi.org/10.1111/j.1461-0248.2005.00836.x

Hartig, F. (2018). *DHARMa: Residual diagnostics for hierarchical multi-level*. Mixed Regression Models.

HilleRisLambers, J., Yelenik, S. G., Colman, B. P., & Levine, J. M. (2010). California annual grass invaders: The drivers or passengers of change? *Journal of Ecology*, *98*(5), 1147–1156. https://doi.org/10.1111/j.1365-2745.2010.01706.x

Hufkens, K., Keenan, T. F., Flanagan, L. B., Scott, R. L., Bernacchi, C. J., Joo, E., … Richardson, A. D. (2016). Productivity of north American grasslands is increased under future climate scenarios despite rising aridity. *Nature Climate Change*, *6*(7), 710–714. https://doi.org/10.1038/nclimate2942

Huisman, J., Jonker, R. R., Zonneveld, C., & Weissing, F. (1999). Competition for light between phytoplankton species: Experimental tests of mechanistic theory. *Ecology*, *80*(1), 211–222.

Huisman, J., & Olff, H. (1998). Competition and facilitation in multispecies plant–herbivore systems of productive environments. *Ecology Letters*, *1*(1), 25–29.

Inouye, R. S., & Tilman, D. (1988). Convergence and divergence of old-field plant communities along experimental nitrogen gradients. *Ecology*, *69*(4), 995–1004.

Jia, S., Wang, X., Yuan, Z., Lin, F., Ye, J., Hao, Z., & Luskin, M. S. (2018). Global signal of top-down control of terrestrial plant communities by herbivores. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(24), 6237–6242. https://doi.org/10.1073/pnas.1707984115

Jutila, H. M., & Grace, J. B. (2002). Effects of disturbance on germination and seedling establishment in a coastal prairie grassland: A test of the competitive release hypothesis. *Journal of Ecology*, *90*(2), 291–302.

Kadmon, R. (1995). Plant competition along soil moisture gradients: A field with experiment the desert annual *Stipa capensis*. *Journal of Ecology*, *83*(2), 253–262.

Kasworm, W. F., Irby, L. R., & Pac, H. B. I. (1984). Diets of ungulates using winter ranges in northcentral Montana. *Journal of Range Management*, *37*(1), 67. https://doi.org/10.2307/3898827

Keesing, F., Allan, B. F., Young, T. P., & Ostfeld, R. S. (2013). Effects of wildlife and cattle on ticks in Kenya. *Ecological Applications*, *23*(6), 1410–1418. Retrieved from http://www.life.illinois.edu/allan/docs/ Keesing et al. 2013 – Effects of wildlife and cattle on ticks in Kenya.Pdf

Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., … Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, *26*(11), 1463–1464. https://doi.org/10.1093/bioinformatics/btq166

Kleinhesselink, A. R., Magnoli, S. M., & Cushman, J. H. (2014). Shrubs as ecosystem engineers across an environmental gradient: Effects on species richness and exotic plant invasion. *Oecologia*, *175*(4), 1277–1290. https://doi.org/10.1007/s00442-014-2972-0

Knapp, A. K., Blair, J. M., Briggs, J. M., Collins, S. L., Hartnett, D. C., Johnson, L. C., & Towne, E. G. (1999). The keystone role of bison in north American tallgrass prairie. *Bioscience*, *49*(1), 39–50. https://doi.org/10.2307/1313492

Koerner, S. E., Burkepile, D. E., Fynn, R. W. S., Burns, C. E., Eby, S., Govender, N., … 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. https://doi.org/10.1890/13-1828.1

Koerner, S. E., Smith, M. D., Burkepile, D. E., Hanan, N. P., Avolio, M. L., Collins, S. L., … Baur, L. E. (2018). Change in dominance determines herbivore effects on plant biodiversity. *Nature Ecology & Evolution*, *2*(12), 1925–1932. https://doi.org/10.1038/s41559-018-0696-y

Kueppers, L. M., Snyder, M. A., Sloan, L. C., Zavaleta, E. S., & Fulfrost, B. (2005). Modelled regional climate change and California endemic oak ranges. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(45), 16281–16286. https://doi.org/10.1073/pnas.0501427102

Lezama, F., Baeza, S., Altesor, A., Cesa, A., Chaneton, E. J., & Paruelo, J. M. (2014). Variation of grazing-induced vegetation changes across a large-scale productivity gradient. *Journal of Vegetation Science*, *25*, 8–21. https://doi.org/10.1111/jvs.12053

Mack, M. C., & Antonio, C. M. D. (1998). Impacts of biological invasions on disturbance regimes. *Trends in Ecology & Evolution*, *13*(5), 195–198.

McCullough, I. M., Davis, F. W., Dingman, J. R., Flint, L. E., Flint, A. L., Serra-Diaz, J. M., … Franklin, J. (2016). High and dry: High elevations disproportionately exposed to regional climate change in Mediterranean-climate landscapes. *Landscape Ecology*, *31*, 1063–1075. https://doi.org/10.1007/s10980-015-0318-x

McNaughton, S. J. (1984). Grazing lawns: Animals in herds, plant form, and coevolution. *American Society of Naturalists*, *124*(6), 863–886. https://doi.org/10.1126/science.26.678.918

McNaughton, S. J., Oesterheld, M., Frank, D. A., & Williams, K. J. (1989). Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature*, *341*, 142–144.

Menezes, B. S., Martins, F. R., Dantas Carvalho, E. C., Souza, B. C., Silveira, A. P., Loiola, M. I. B., & Araújo, F. S. (2020). Assembly rules in a resource gradient: Competition and abiotic filtering determine the structuring of plant communities in stressful environments. *PloS One*, *15*(3), e0230097.

Milchunas, D. G., & Lauenroth, W. K. (1993). Quantitative effects of grazing on vegetation and soils over a global range of environments: Ecological archives M063-001. *Ecological Monographs*, *63*(4), 327–366.

Milchunas, D. G., & Noy-Meir, I. (2002). Grazing refuges, external avoidance of herbivory and plant diversity. *Oikos*, *99*(1), 113–130.

Milchunas, D. G., Sala, O. E., & Lauenroth, W. K. (1988). A generalized model of the effects of grazing by large herbivores on grassland community structure. *The American Naturalist*, *132*(1), 87–106. https://doi.org/10.1086/284839

Molinari, N. A., & D'Antonio, C. M. (2020). Where have all the wildflowers gone? The role of exotic grass thatch. *Biological Invasions*, *22*(3), 957–968.

Mwendera, E. J., Mohamed Saleem, M. A., & Dibabe, A. (1997). The effect of livestock grazing on surface runoff and soil erosion from sloping pasture lands in the Ethiopian highlands. *Australian Journal of Experimental Agriculture*, *37*(4), 421–430. https://doi.org/10.1071/EA96145

Myers, N., Mittermeler, R. A., Mittermeler, C. G., Da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*(6772), 853–858. https://doi.org/10.1038/35002501

Odadi, W. O., Karachi, M., Abdulrazak, S. A., & Young, T. P. (2011). African wild ungulates compete with or facilitate cattle depending on season. *Science*, *333*(6050), 1753–1755. https://doi.org/10.1126/science.1208468

Oksanen, A., Siles-Lucas, M., Karamon, J., Possenti, A., Conraths, F. J., Romig, T., … Casulli, A. (2016). The geographical distribution and prevalence of *Echinococcus multilocularis* in animals in the European Union and adjacent countries: A systematic review and meta-analysis. *Parasites & Vectors*, *9*(1), 519. https://doi.org/10.1186/s13071-016-1746-4

Olff, H., & Ritchie, M. E. (1998). Effects of herbivores on grassland plant diversity. *Trends in Ecology & Evolution*, *13*(7), 261–265. https://doi.org/10.1016/S0169-5347(98)01364-0

Orr, D., Bui, A., Klope, M., McCullough, I. M., Lee, M., Motta, C., Mayorga, I., Konicek, K., & Young, H. S. (2022). Context-dependent effects of shifting large herbivore assemblages on plant structure and diversity. Dryad Digital Repository, https://doi.org/10.25349/D94W48

Osem, Y., Perevolotsky, A. V. I., & Kigel, J. (2002). Grazing effect on diversity of annual plant communities in a semi-arid rangeland: Interactions with small-scale spatial and temporal variation in primary productivity. *Journal of Ecology*, *90*, 936–946.

Osem, Y., Perevolotsky, A. V. I., & Kigel, J. (2004). Site productivity and plant size explain the response of annual species to grazing exclusion in a Mediterranean semi-arid rangeland. *Journal of Ecology*, *92*, 297–309.

Porensky, L. M., Wittman, S. E., Riginos, C., & Young, T. P. (2013). Herbivory and drought interact to enhance spatial patterning and diversity in a savanna understory. *Oecologia*, *173*(2), 591–602. https://doi.org/10.1007/s00442-013-2637-4

Prins, A. H., Nell, H. W., & Klinkhamer, P. G. L. (1992). Size-dependent root herbivory on *Cynoglossum officinale*. *Oikos*, *65*(3), 409–413.

Prins, H. H. T. (2000). Competition between wildlife and livestock in Africa. In *Wildlife conservation by sustainable use* (pp. 51–80). Springer. https://doi.org/10.1007/978-94-011-4012-6

Proulx, M., & Mazumder, A. (1998). Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology*, *79*(8), 2581–2592.

R Core Team. (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Richter, C. J. (2015). *Influence of functional traits, shrub neighbors, and habitat types on plant responses to herbivores*. Sonoma State University.

Sitters, J., Wubs, E. R. J., Bakker, E. S., Crowther, T. W., Adler, P. B., Bagchi, S., … Seabloom, E. W. (2020). Nutrient availability controls the impact of mammalian herbivores on soil carbon and nitrogen pools in grasslands. *Global Change Biology*, *26*(4), 2060–2071. https://doi.org/10.1111/gcb.15023

Soofi, M., Ghoddousi, A., Zeppenfeld, T., Shokri, S., Soufi, M., Jafari, A., … Waltert, M. (2018). Livestock grazing in protected areas and its effects on large mammals in the Hyrcanian forest. *Iran. Biological Conservation*, *217*(June), 377–382. https://doi.org/10.1016/j.biocon.2017.11.020

Sork, V. L., Davis, F. W., Westfall, R., Flint, A., Ikegami, M., Wang, H., & Grivet, D. (2010). Gene movement and genetic association with regional climate gradients in California valley oak (*Quercus lobata* Née) in the face of climate change. *Molecular Ecology*, *19*(17), 3806–3823. https://doi.org/10.1111/j.1365-294X.2010.04726.x

Spasojevic, M. J., & Suding, K. N. (2012). Inferring community assembly mechanisms from functional diversity patterns: The importance of multiple assembly processes. *Journal of Ecology*, *100*(3), 652–661.

Stahlheber, K. A., & Antonio, C. M. D. (2013). Using livestock to manage plant composition: A meta-analysis of grazing in California Mediterranean grasslands. *Biological Conservation*, *157*, 300–308. https://doi.org/10.1016/j.biocon.2012.09.008

Stevens, J. T., Safford, H. D., Harrison, S., & Latimer, A. M. (2015). Forest disturbance accelerates thermophilization of understory plant communities. *Journal of Ecology*, *103*, 1253–1263. https://doi.org/10.1111/1365-2745.12426

Suominen, O., Niemelä, J., Martikainen, P., Niemelä, P., & Kojola, I. (2003). Impact of reindeer grazing on ground-dwelling Carabidae and Curculionidae assemblages in Lapland. *Ecography*, *26*(4), 503–513. https://doi.org/10.1034/j.1600-0587.2003.03445.x

Tilman, D. (1982). *Resource competition and community structure*. Princeton University Press.

Tilman, D., HilleRisLambers, J., Harpole, S., Dybzinski, R., Fargione, J., Clark, C., & Lehman, C. (2004). Does metabolic theory apply to community ecology? It's a matter of scale. *Ecology*, *85*(July), 1797–1799.

Tucker, C. M., Cadotte, M. W., Carvalho, S. B., Davies, T. J., Ferrier, S., Fritz, S. A., … Lanna, S. (2017). A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biological Reviews*, *92*(2), 698–715. https://doi.org/10.1111/brv.12252

van der Plas, F., Howison, R. A., Mpanza, N., Cromsigt, J. P., & Olff, H. (2016). Different-sized grazers have distinctive effects on plant functional composition of an A frican savannah. *Journal of Ecology*, *104*(3), 864–875.

Veblen, K. E., Porensky, L. M., Riginos, C., & Young, T. P. (2016). Are cattle surrogate wildlife? Savanna plant community composition explained by total herbivory more than herbivore type. *Ecological Applications*, *26*(6), 1610–1623.

Venail, P., Gross, K., Oakley, T. H., Narwani, A., Allan, E., Flombaum, P., … Cardinale, B. J. (2015). Species richness, but not phylogenetic diversity, influences community biomass production and temporal stability in a re-examination of 16 grassland biodiversity studies. *Functional Ecology*, *29*(5), 615–626. https://doi.org/10.1111/1365-2435.12432

Violle, C., Garnier, E., Lecoeur, J., Roumet, C., Podeur, C., & Navas, A. B. M. (2009). Competition, traits and resource depletion in plant communities. *Community Ecology*, *160*, 747–755. https://doi.org/10.1007/s00442-009-1333-x

Vitousek, P. M. (1986). Biological invasions and ecosystem properties: Can species make a difference? In *Ecology of biological invasions of North America and Hawaii* (pp. 163–176). Springer.

Vojtech, E., Turnbull, L. A., & Hector, A. (2007). Differences in light interception in grass monocultures predict short-term competitive outcomes under productive conditions. *PLoS ONE*, *6*, e499. https://doi.org/10.1371/journal.pone.0000499

WallisDeVries, M. F., Bakker, J. P., & Van Wieren, S. E. (1998). *Grazing and conservation management*. Springer Science & Business Media.

Webb, C. O., & Donoghue, M. J. (2005). Phylomatic: Tree assembly for applied phylogenetics. *Molecular Ecology Notes*, *5*(1), 181–183. https://doi.org/10.1111/j.1471-8286.2004.00829.x

Wedin, D., & Tilman, D. (1993). Competition among grasses along a nitrogen gradient: Initial conditions and mechanisms of competition. *Ecological Monographs*, *63*(2), 199–229.

Western Regional Climate Center. (2015). Desert Research Institute. Retrieved from http://www.wrcc.dri.edu/

Young, H. S., Dirzo, R., Helgen, K. M., McCauley, D. J., Billeter, S. A., Kosoy, M. Y., … Dittmar, K. (2014). Declines in large wildlife increase landscape-level prevalence of rodent-borne disease in Africa. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(19), 7036–7041. https://doi.org/10.1073/pnas.1404958111

Young, H. S., McCauley, D. J., Galetti, M., & Dirzo, R. (2016). Patterns, causes, and consequences of Anthropocene defaunation. *Annual Review of Ecology, Evolution, and Systematics*, *47*(August), 333–358. https://doi.org/10.1146/annurev-ecolsys-112414-054142

Young, H. S., Mccauley, D. J., Helgen, K. M., Goheen, J. R., Otárola-castillo, E., Palmer, T. M., … Dirzo, R. (2013). Effects of mammalian herbivore declines on plant communities: Observations and experiments in an African savanna. *Journal of Ecology*, *101*, 1030–1041. https://doi.org/10.1111/1365-2745.12096

Young, T. P., Okello, B., Kinyua, D., & Palmer, T. M. (1997). KLEE: A long-term multi-species herbivore exclusion experiment in Laikipia, Kenya. *African Journal of Range and Forage Science*, *14*, 92–104.

Zhu, M., Pan, Y., Huang, Z., & Xu, P. (2016). An alternative method to predict future weather data for building energy demand simulation under global climate change. *Energy & Buildings*, *113*, 74–86. https://doi.org/10.1016/j.enbuild.2015.12.020

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 Science & Business Media. Retrieved from http://arxiv.org/abs/1305.6995

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Orr, D. A., Bui, A., Klope, M., McCullough, I. M., Lee, M., Motta, C., Mayorga, I., Konicek, K. & Young, H. S. (2022). Context-dependent effects of shifting large herbivore assemblages on plant structure and diversity. *Journal of Ecology*, *110*, 1312–1327. https://doi.org/10.1111/1365-2745.13871