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Interactions among multiple drivers of global change: climate-mediated effects of wild and domestic herbivores on plant communities and ecosystem function in southcentral California

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Interactions among multiple drivers of global change: climate-mediated effects of wild and domestic herbivores on plant communities and ecosystem function in southcentral California

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Ecology, Evolution, and Marine Biology

by

Devyn Ainsley Orr

Committee in charge:
Professor Hillary Young, Chair
Professor Carla D'Antonio
Professor Lauren Ponisio

June 2021

The dissertation of Devyn Ainsley Orr is approved.

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June 2021

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VITA OF DEVYN AINSLEY ORR

June 2021

EDUCATION

2021	**Ph.D.,** Community Ecology. University of California, Santa Barbara, Dept. Ecology, Evolution, and Marine Biology. Advisor: Dr. Hillary Young
2010	**B.A.,** ***High Honors***, Biology. University of California, Santa Barbara, College of Creative Studies, emphasis in Ecology, Evolution, and Marine Biology

PROFESSIONAL EXPERIENCE

2020	**Instructor of Record.** Ecology and Conservation of Terrestrial Vertebrates (EEMB 113L). Department of Ecology, Evolution, and Marine Biology. University of California Santa Barbara (UCSB).
2019-2021	**Graduate Researcher.** National Science Foundation (NSF) Division of Environmental Biology (DEB) Award #1900502. University of California Santa Barbara (UCSB).
2019-2021	**Graduate Researcher**. National Geographic Society Committee for Research and Exploration. University of California Santa Barbara (UCSB).
2017-2021	**Graduate Research Fellow.** NDSEG, Department of Ecology, Evolution, and Marine Biology. University of California Santa Barbara (UCSB).
2014-2017	**Teaching Assistant.** Department of Ecology, Evolution, and Marine Biology. University of California Santa Barbara (UCSB).
2014-2020	**Biological Field Technician**. Western Foundation of Vertebrate Zoology, Camarillo, CA, in contract with The Nature Conservancy, Ventura Co., CA. (limited term: project-based contract)
2012-2015	**Biological Field Technician.** Stillwater Sciences, Berkeley, CA. (limited term: on call)
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2011	**Scientific Visualization Fellow**. Valentine Camp, University of California Natural Reserve System, Mammoth Lakes, CA (limited term: summer)
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2010-2011	**Assistant Project Manager**. Santa Clara River Restoration Project. Marine Science Institute, University of California Santa Barbara (UCSB).

2007-2010 **Independent Student Researcher**. Marine Science Institute, University of California Santa Barbara (UCSB).

2007-2008 **Research Assistant**. Marine Science Institute, University of California Santa Barbara (UCSB).

2007-2009 **Research Assistant.** Department of Physical Anthropology. University of California Santa Barbara (UCSB).

2007, 2008 **Curatorial Assistant**. Museum of Vertebrate Zoology, University of California Berkeley. (limited term: summer)

PEER-REVIEWED PUBLICATIONS

** Undergraduate mentee co-author; † Authors in alphabetical order with equal contribution*

Journal Articles

2021 1. Parsons, J*, C Motta*, A Miller-ter-Kuile, H Young, **D Orr**. Interactive effects of large herbivores and climate on California oak regeneration. *Forest Ecology and Management*. In revision.

2. D Orr, Z Zils, E Duge*, S Copeland*, A Bui*, C Motta*, A Swei, and H Young. Climate-dependent effects of livestock and wildlife on tick survivorship in California. *Journal of Applied Ecology*. In revision.

3. A Miller-ter-Kuile, A Apigo, A Bui, B DiFiore, E Forbes, M Lee**, D Orr,** D Preston, R Behm, T Bogar, J Childres, R Dirzo, M Klope, Kevin Lafferty, John McLaughlin, M Morse, C Motta, K Park, K Plummer, D Weber, R Young, H Young. Predator-prey interactions of terrestrial invertebrates are determined by predator body size and species identity. *Ecology*. In review.

4. D Orr, A Bui*, M Klope, I McCullough, M Lee*, C Motta*, I Mayorga*, K Konicek* and H Young. Effects of realistic shifts in large herbivore assemblages on plant structure and diversity vary across climates. *Journal of Ecology*. In press.

2020 5. Bui, A.*, **D. Orr**, M. Lepori-Bui, K. Konicek*, H. Young, H. Moeller. 2020. Soil fungal community composition and functional similarity shift across distinct climatic conditions. *FEMS Microbiology Ecology*, fiaa193, https://doi.org/10.1093/femsec/fiaa193

6. Miller-ter Kuile, A., **D. Orr**, A. Bui*, R. Dirzo, M. Klope, D. McCauley, C. Motta*, H. Young. 2020. Impacts of rodent eradication on seed predation and plant community biomass on a tropical atoll. *Biotropica*, https://doi.org/10.1111/btp.12864

7. Hardesty-Moore, M, **D. Orr**, D. McCauley. 2020. Invasive plant *Arundo donax* alters habitat use by carnivores. *Biological Invasions.* (2)1-13. https://doi.org/10.1007/s10530-020-02234-4.

2018 8. Hardesty-Moore, M, S. Deinet, R. Freeman, G. Titcomb, E. Dillon, K. Stears, M. Klope, A. Bui*, **D. Orr**, H. Young, A. Miller-ter Kuile, L. Hughey, D. McCauley. 2018. Migration in the Anthropocene: how collective navigation, environmental system, and taxonomy shape the vulnerability of migratory species. *Phil. Trans. B: Biological Sciences*. 373: 20170017. https://doi.org/10.1098/rstb.2017.0017.3

2016	9. †Forbes, E., †Miller-ter-Kuile, A., †**Orr, D.A**., and †G.E. Titcomb. 2016. Navigating the Cascades of Circumstance. *Science.* 352(6289): 1062. https://doi.org/10.1126/science.aaf7138.

Technical Reports

2017	Orr, B.K., Leverich, G. L., Diggory, Z. E., Dudley, T. L., Hatten, J. R., Hultine, K. R., Johnson, M. P., **Orr**, **D.A.** and S. Stone. 2017. Large-scale Riparian Restoration Planning and Implementation on the Virgin and Gila Rivers. U.S. Geological Survey Open-File Report: Case studies of riparian and watershed restoration in the southwestern United States—Principles, challenges, and successes. 2017-1091, p.77-83. https://doi.org/10.3133/20171091.
2014	Orr, B.K., Leverich, G. L., Diggory, Z. E., Dudley, T. L., Hatten, J. R., Hultine, K. R., Johnson, M. P., and **D.A. Orr**. 2014. Riparian Restoration Framework for the Upper Gila River, Arizona. U.S. Geological Survey Open-File Report.

Datasets

2018	A Miller-ter Kuile, **D. Orr,** A. Bui, R. Dirzo, M. Klope, D. McCauley, C. Motta^{+}, H. Young. 2019. Impacts of rodent eradication on seed predation and plant community biomass. *Mendeley Data*. v1. https://doi.org/10.17632/d7jk36hhyy.1.

FELLOWSHIPS, AWARDS, AND HONORS

Fellowships

2017-2021	National Defense Science and Engineering Graduate Research Fellowship **($153,600)**
2015-2016	STEM Fellowship, UC Santa Barbara **($24,000)**
2014-2015	Graduate Opportunity Fellowship, UC Santa Barbara **($27,000)**

Awards and Honors

2019	Travel Award, Department of Defense Graduate Research Conference, San Diego **($782)**
2018	Travel Award, Nutrient Network Annual Meeting, University of Minnesota **($553)**
2017	Fiona Goodchild Mentorship Award, UC Santa Barbara; for excellence in undergraduate research mentorship **($800)**
2017	Mildred Mathias Educational Research Award, UC Natural Reserve System (with Ana Miller-ter-Kuile) **($153)**
2017	UC LEADS Summer Student Mentorship Award, University of California **($800)**
2016	EUREKA Summer Student Mentorship Award, California Nanosystems Institute **($800)**
2015	Worster Summer Mentorship Award, UC Santa Barbara **($5000)**
2010	University High Honors, UC Santa Barbara
2010	Henry W. Offen Memorial Endowment Award, UC Natural Reserve System **($1800)**
2009	Watson Award for Undergraduate Research, UC Santa Barbara **($2700)**
2008	Undergraduate Research and Creative Activities Award, UC Santa Barbara **($500)**

CONFERENCE PRESENTATIONS

2020	“Throwing shade: large mammalian herbivores alter survival of arthropod disease vectors through changes in understory vegetation, but effects are density and climate dependent.” Ecological Society of America Annual

	Meeting: Effects of Multiple Global Changes on Communities and Ecosystems. Oral Session (virtual).
2019	“Herbivore density and identity matters for plant productivity-richness relationships in southcentral California.” Gordon Research Conference: Plant-Herbivore Interactions.
2019	“Large mammals impact tick abundance and survivorship in a California rangeland.” Western Section of the Wildlife Society Annual Meeting: Pathogens and Invasive Species. Oral Session.
2017	“Interactive effects of large mammal loss and climate change on ecosystem processes: the Tejon Ranch Exclosure Experiment.” Ecological Society of America Annual Meeting: Effects of Multiple Global Changes on Communities and Ecosystems. Oral Session.
2016	“Tamarisk, water, beetles, and birds: The importance of vegetation in addressing the challenges of managing novel riparian ecosystems in the arid west.” Ecological Society of America Annual Meeting: Novel Ecosystems as Described, Defined, and Monitored Using the National Vegetation Classification. Oral Session.
2015	“Effects of changing climate and wildlife communities on tick-borne disease in California.” 11th Annual EEMB Graduate Student Symposium, University of California Santa Barbara. Invited Speaker.
2014	“An Ecohydrological Approach to Riparian Restoration Planning in the American Southwest.” American Geophysical Union.
2011	“Avian response to *Arundo donax* invasion on the Lower Santa Clara River, California.” 53rd Western Section Annual Conference, The Wildlife Society, Ecology and Management of Invasive Species Session, Riverside California. Invited Speaker.

ABSTRACT

Interactions among multiple drivers of global change: climate-mediated effects of wild and domestic herbivores on plant communities and ecosystem function in southcentral California

by

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Ecosystems around the world are being profoundly altered by anthropogenic global change. Two prominent and interacting drivers of global change in grassland and savanna ecosystems are climate change and changing large herbivore communities, specifically declining populations of wild ungulates and their replacement with livestock. In the face of these shifts, understanding how climatic conditions mediate herbivore control of ecosystem structure and function is imperative, particularly on rangelands, which cover almost a third of the United States and an estimated 50% of ice-free land globally. I initiated a large-scale herbivore exclosure experiment, replicated across a topoclimatic gradient in Kern Co., CA to investigate 1) the effects of both wild ungulates and cattle on plant community diversity and vegetation structure, and 2) whether the magnitude or direction of herbivore impacts varies depending on climatic context. I demonstrate the cascading consequences of wild ungulate 'loss' and domestic herbivore 'introduction', by investigating a) the consequences of ungulate-mediated change in vegetation structure on microclimatic conditions and larval tick survival, and b) how shifts in plant composition and diversity alter the availability of floral resources (i.e., nectar) for pollinators. These studies demonstrate pathways by which both wild and domestic herbivores can have significant impacts on vital ecosystem functions, disease transmission and pollination, and how these impacts will likely vary with climate. This work improves our ability to understand and predict the consequences of compounding drivers of global change on the structure and function of savanna ecosystems within and beyond California.

TABLE OF CONTENTS

CHAPTER 1: INTRODUCTION

We, as humans, are profoundly impacting this planet. The main drivers of human-driven global environmental change (including climate, land use) are resulting in biodiversity change (both introductions and losses) at unprecedented rates (Barnosky et al. 2011, Hughes et al. 2013). These global change drivers are not only altering biodiversity patterns (Pimm et al 2014), but are also having pervasive impacts on interactions among species, often altering competitive dynamics among both plants and animals, including among groups that play crucial roles in structuring ecosystems (Valiente-Banuet et al. 2015). These species interactions can exert multitrophic effects that ripple across food webs, shaping a myriad of ecosystem functions (Schulze and Mooney 2012; Dirzo et al 2014), and these functions often change even before species or interactions completely disappear (Galetti et al. 2013, Rozas-Davila et al. 2016).

Despite the significant consequences of these shifts in biodiversity and species interactions, syntheses of global change impacts have found substantial variability among studies in both the magnitude and direction of effects of any given global driver on any given type of biotic interaction (Tylianakis et al., 2008). Further, the synergistic effects among multiple drivers acting simultaneously create challenges in predicting future responses to global environmental change, and extrapolating these complex impacts across entire networks of species remains challenging, with results that we are still struggling to anticipate. Thus, in order to reliably predict the effects of global environmental change on community and ecosystem processes, the greatest single challenge facing ecologists remains determining how biotic and abiotic context alters the direction and magnitude of global change effects on biotic interactions (Tylianakis et al., 2008; Chamberlain et al. 2014).

In this dissertation, I aim to aid in filling this research gap by investigating three of the most prominent forms of global change occurring today: 1) declining populations of large-bodied wildlife, 2) livestock introductions and conversion of wildland to rangeland and 3) climate change. Over the last decade, ecologists have gained important insight into the ecological effects of these wildlife declines, demonstrating that this phenomenon is not merely a conspicuous consequence of human impacts on the planet, but is also a driver of global change in its own right (Dirzo et al., 2014), with impacts on nutrient movement, climate regimes, and energy flow (Forbes, Cushman, Young, Klope, & Young, 2019; Ripple et al., 2014; H. S. Young, McCauley, Galetti, & Dirzo, 2016). Yet efforts to understand and, critically, to predict the consequences of this Anthropocene defaunation event have been deeply hindered by the complex and context-dependent nature of community responses to biotic disturbance. Since defaunation is not occurring in isolation, but rather alongside other dominant global change drivers, its impacts on ecosystems likely vary as a result of interactions with other forms of human disturbance, most notably climate change. Indeed, prior studies have demonstrated that the functional roles of large wildlife are highly dependent on climatic context, which often mediates the strength or outcome of their interactions in a community (Augustine & McNaughton, 2006; Bakker et al., 2006; Goheen et al. 2013; Borer et al., 2014). Thus, there is strong potential for synergies among wildlife loss and climate change, potentially amplifying the impacts of wildlife loss on ecosystem structure and function. Further hindering our understanding of defaunation’s consequences is the fact that biodiversity change in the Anthropocene is not merely a story of loss: in many systems, including California, native wildlife have been replaced by introduced, largely commensal, megafauna (livestock), leading to community turnover (Barnosky 2009). Global increases in livestock have more than compensated, by biomass, for wildlife loss; rangelands now accounts for roughly 30% of the world’s ice-free land surface and livestock outweigh wildlife by a factor of 10 (Bar-On et al., 2018). Given this pattern, to adequately consider the likely future interactions between climate change and megafaunal change, it is critical to consider both isolated large wildlife loss, and the potential for compensation associated with increases in livestock.

In the following chapters, I investigate interactions among wildlife declines, livestock additions, and changing climatic conditions using a large-scale herbivore exclosure experiment that I established in Kern Co., CA. “Exclosures” are a widely used method to understand the ecological ramifications of large herbivore declines or additions (e.g. Goheen et al. 2013; Forbes et al. 2019). This experiment uses complete and semi-permeable herbivore exclosures to explore differences among sites with wild herbivores only, with wild herbivores and livestock, and with no large herbivores. To understand variation in effects across climatic contexts, the experiment is replicated along a montane topoclimate gradient. I examine the interactive effects of both wildlife and livestock on plant communities and cascading effects on ecosystem function across a range of climatic contexts that approximates the range of climate variation expected to occur in our study region over the next 50-100 years (McCullough et al., 2015).

This work improves our projections of future oak savanna landscapes regionally, and provides a valuable framework for integrating wildlife and livestock management decisions with biodiversity and zoonotic disease management. Most broadly, findings provide insight into how multiple forms of global change can interact to amplify anthropogenic effects on ecosystem function (here, disease mitigation and pollination).

Chapter Overviews:

This dissertation has three parts, each of which discusses a different aspect of the community ecology of a semi-arid California savanna. The two prominent themes are the context-dependence of herbivore impacts on savanna communities, and the prevalence of cascading indirect effects. The research for all chapters was conducted at Tejon Ranch in Kern County, California, USA.

My second chapter directly compares the consequences of changes in herbivore assemblages on herbaceous vegetation structure and diversity. I show that vegetation structure responds primarily to herbivore treatment regardless of climate. In contrast, I find that large herbivores can have positive or negative effects on plant diversity depending on climatic context and the herbivores present (wild, vs wild and domestic). I demonstrate that, as predicted by established theory, climate can mediate the effects of large herbivores on plant community richness and diversity, but this varies by herbivore guild, with cattle driving stronger effects than wildlife, likely due to a combination of higher densities and differences in diet. Furthermore, livestock presence produced effect directions opposite those expected based on prior experiments using wildlife-only manipulations. Thus, interactions among realistic shifts in herbivores and climate can produce novel results.

My third chapter investigates the cascading effects of climate and large herbivores on tick survivorship, with implications for tickborne disease. I show that through indirect pathways, large herbivores have strong suppressive impacts on tick survivorship. Increases in plant cover and standing biomass ameliorate microclimate conditions at the soil surface, extending survivorship times for juvenile tick life stages while off-host, with stronger effects under more arid conditions. Extended survival times increase the chance for ticks to successfully obtain a bloodmeal; thus these results have important implications for disease management in the far western U.S.

My fourth chapter builds upon the plant diversity responses I observed in chapter two by investigating how plant composition changes impact floral resource availability for insect pollinators. I demonstrate that the changes in plant composition lead to differences in floral density, diversity, and ultimately, production of nectar sugars. These results show that large herbivores have significant impacts on floral resource availability, and these impacts are mediated by climate.

Chapter 2 has been accepted at *Journal of Ecology* and is currently in press. Chapter 3 is currently in revision at *Journal of Applied Ecology*. Likewise, Chapter 4 is being prepared for submission this summer. I strongly urge readers to consult the final published versions of these works.

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Extinction of Birds Drives Rapid Evolutionary Changes in Seed Size. Science 340:1086–1091.

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CHAPTER 2: CONTEXT-DEPENDENT EFFECTS OF SHIFTING LARGE HERBIVORE ASSEMBLAGES ON PLANT STRUCTURE AND DIVERSITY

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2.1 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 these changes in herbivore composition and density have on plant communities, particularly when combined with ongoing concurrent changes in climate. Considering these prominent forms of global change in tandem enables us to better understand controls on savanna plant communities under real-world conditions.

2. We conducted a field-based experiment directly comparing the consequences of two commonly occurring changes in herbivore assemblages on savanna vegetation structure and diversity. Specifically, we used complete and semi-permeable herbivore exclosures to explore the difference in plant communities among sites with wild herbivores only, with livestock 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 topoclimate gradient in California.

3. We found that 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 aboveground biomass, while the addition of livestock 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. Livestock had a neutral to strongly negative effect at low aridity, but a strong positive effect at high aridity. These results suggest that 1) herbivore effects can override climate effects on vegetation structure, 2) livestock addition can drive different effects on diversity 3) herbivore effects on diversity are modulated by climate.

4. Our results illustrate very distinctive shifts in plant communities between two realistic forms of changes in historic ungulate herbivore assemblages—livestock addition and isolated large herbivore losses—particularly for plant diversity responses, and also 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 that climate regimes are changing globally.

2.2. 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, Cushman, Young, Klope, & Young, 2019; Ripple et al., 2014; H. S. Young, McCauley, Galetti, & Dirzo, 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, Knapp, Briggs, Blair, & Steinauer, 1998; Jia et al., 2018; Knapp et al., 1999; McNaughton, Oesterheld, Frank, & Williams, 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, Porensky, Riginos, Veblen, & Young, 2017; Cleland et al., 2019; Fay et al., 2015; Stevens, Safford, Harrison, & Latimer, 2015), disease transmission (Keesing, Allan, Young, & Ostfeld, 2013; H. S. Young et al., 2014), and soil and plant elemental pools and fluxes (Crowther et al., 2019; Firn, Nguyen, Schütz, & Risch, 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, Bakker, & Van Wieren, 1998), while being simultaneously introduced to others, predominantly as livestock (Barnosky, 2008; Knapp et al., 1999; Milchunas, Sala, & Lauenroth, 1988; Wardle, Barker, Yeates, & Bonner, 2001), but also as feral invasives (e.g. *Sus scrofa*, Mack & Antonio, 1998; Vitousek, 1986). Livestock now account for sixty percent of all mammalian life on Earth, equaling approximately a trillion kilograms in biomass (Bar-On, Phillips, & Milo, 2018). This is exponentially increasing large herbivore densities from pre-human baselines across the globe (Barnosky, 2008), particularly in arid and semiarid grasslands which compose over a third of the world’s rangelands (de Haan, Steinfeld, & Blackburn, 1997). This trajectory is likely to continue to accelerate as landscapes become increasingly human-dominated (Figure 1).

Understanding the ramifications of such shifts in large herbivore assemblages requires empirical investigation of these density- and identity-driven impacts on plant

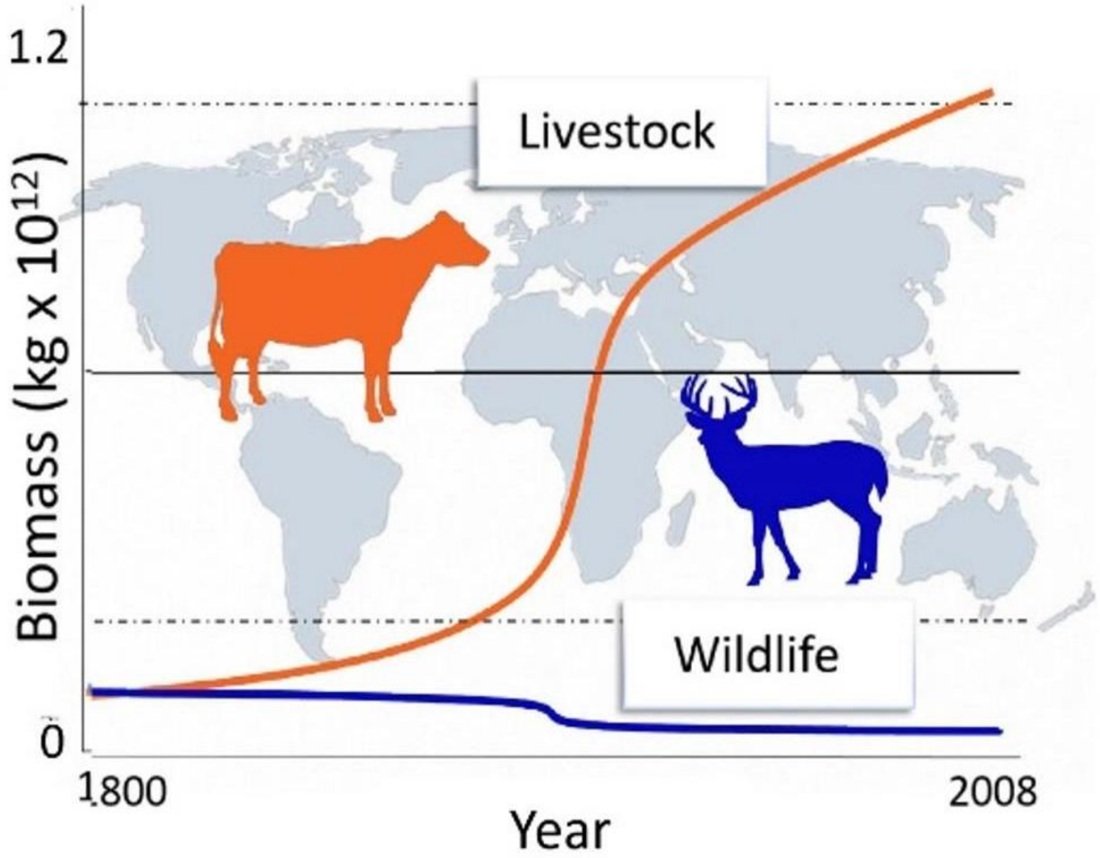

Figure 1: Global declines in wildlife and additions of livestock

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, Phillips, & Milo, 2018 and graphically interpreted by D. Orr.

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 (for example, Bakker, Ritchie, & Olff, 2006; Borer, Seabloom, Gruner, & Harpole, 2014; Koerner et al. 2018; Gao & Carmel 2020), 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, Wittman, Riginos, & Young, 2013; Veblen, Porensky, Riginos, & Young, 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, Wittman, Riginos, & Young, 2013; Veblen, Porensky, Riginos, & Young, 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, Herrero, Conant, Sircely, & Thornton, 2018). Therefore, developing a better understanding of the role of climatic conditions in modulating herbivory effects will be increasingly important (Milchunas & Lauenroth, 1993; Osem, Perevolotsky, & Kigel, 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 influencing 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 (Odho & Takahashi., 2020) 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, Jonker, Zonneveld, & Weissing, 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, Elberse, & Geerts, 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 homogenous 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 1) they are experiencing rapid concomitant changes in ungulate assemblages and climate, 2) they have been the focus of extensive climate change experiments and modeling (e.g. Bartolome, Barry, Griggs, & Hopkinson, 2007; Davis et al., 2019; Dudney et al., 2017; Zhu, Pan, Huang, & Xu, 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: (1) 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)? (2) 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? (3) Can the impacts of wild and domestic herbivore on plant species dominance explain plant diversity responses? We hypothesized: (1) 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; (2) aridity differences across sites will result in a pattern of herbivores (i) exerting stronger effects on structure at higher aridity. Finally, (3) 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.

2.3. METHODS

2.3.1. 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 hectares 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 1500-1600 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 overstory at the study area is primarily composed of three species of oak *(Quercus douglasii, Q. lobata, Q. kelloggii*), with *Q. douglasii* dominating hot, dry savanna foothill sites, and *Q. kellogii* 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 1372 m.

2.3.2. *Exclosure Experiment Design*

Our exclosure experiment is located at the site of prior research measuring and modeling 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

580-1650m (Figure 2; more details in Appendix 1). At each of the three climatically distinct levels – Arid (580 m elevation), Intermediate (1650m, south-facing slope), and Mesic (1650m, 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 40kg body mass with complete barriers, wild ungulates (partial exclosure) which used semi-permeable fencing to remove cattle, and wildlife + cattle (control) (Figure 2a).

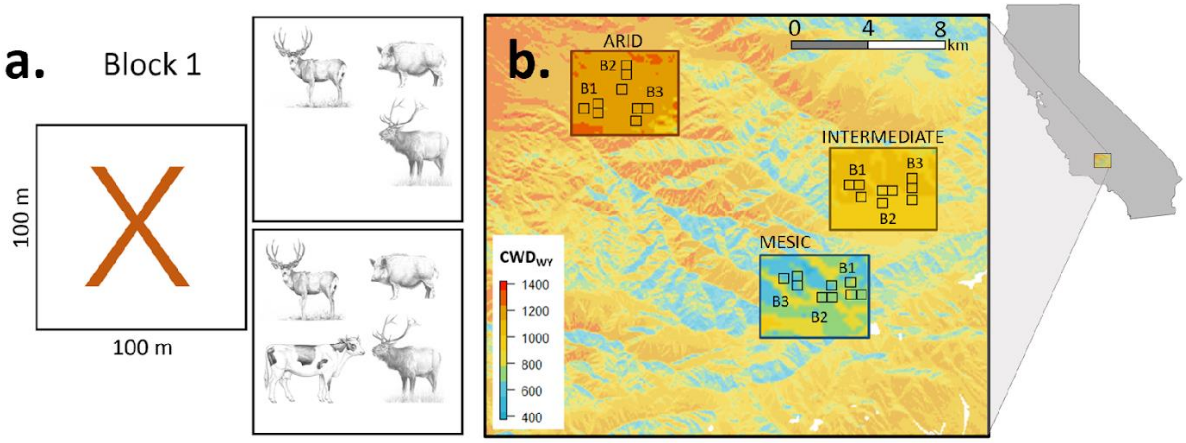

Figure 2: Block schematic and map of large herbivore treatments used in the Tejon Ranch Exclosure Experiment (TREE)

A) The experiment utilizes 9 blocks, each consisting of 3 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 x 100 m). B) The 9 blocks are clustered across three aridity levels (Arid, Intermediate, 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.

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 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 in order 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 this is design issue is of minimal concern (for an evaluation of site-level conditions, see Appendix 1).

2.3.3. Herbivore Activity and Exclosure Efficacy

In each plot, we measured dung densities of wild ungulates and cattle along three 100 m x 4 m belt transects each spring (April-June), summer (July-September), fall (October- November) and winter (December-March), from 2017-2018. 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 details in Appendix 1.

2.3.4. Investigating Herbivore x Aridity Effects on Plant Communities

We focused on plant community responses that have been associated with downstream changes in ecosystem function, including 1) vegetation structural characteristics and 2) 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 (in order 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 understory vegetation (HilleRisLambers, Yelenik, Colman, & Levine, 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, Core Development 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 calculated MPD for each community using the picante package (Kembel et al., 2010; additional methods in Appendix 1).

2.3.5. *Sampling design*

We surveyed plots in 2019, three 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 two 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 1ha plot (similar in design to Goheen et al., 2013), and visually estimated species cover in 1 x 1 m subplots spaced every 10m 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 x 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, Goldman, Keil, Patterson, & Rosatti, 2012).

We evaluated shading by measuring the difference between photosynthetically active radiation (ΔPAR) above and below understory vegetation in ten 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 am and 2:00 pm, 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, Turnbull, & Hector, 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 x 0.25 m subplots within each plot, drying the biomass (60 °C for 72 h), and weighing it.

Figure 3: Herbivore treatment effects on aboveground biomass.

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.

2.3.6 *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, Ieno, Walker, Saveliev, & Smith, 2009). We fit all models using the lme4 package (Bates, Kliegl, Vasishth, & Baayen, 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^2m”) and conditional (hereafter “R^2c”) 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.

2.4. RESULTS

2.4.1. 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 (Fig 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 1). 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 behavior, 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.

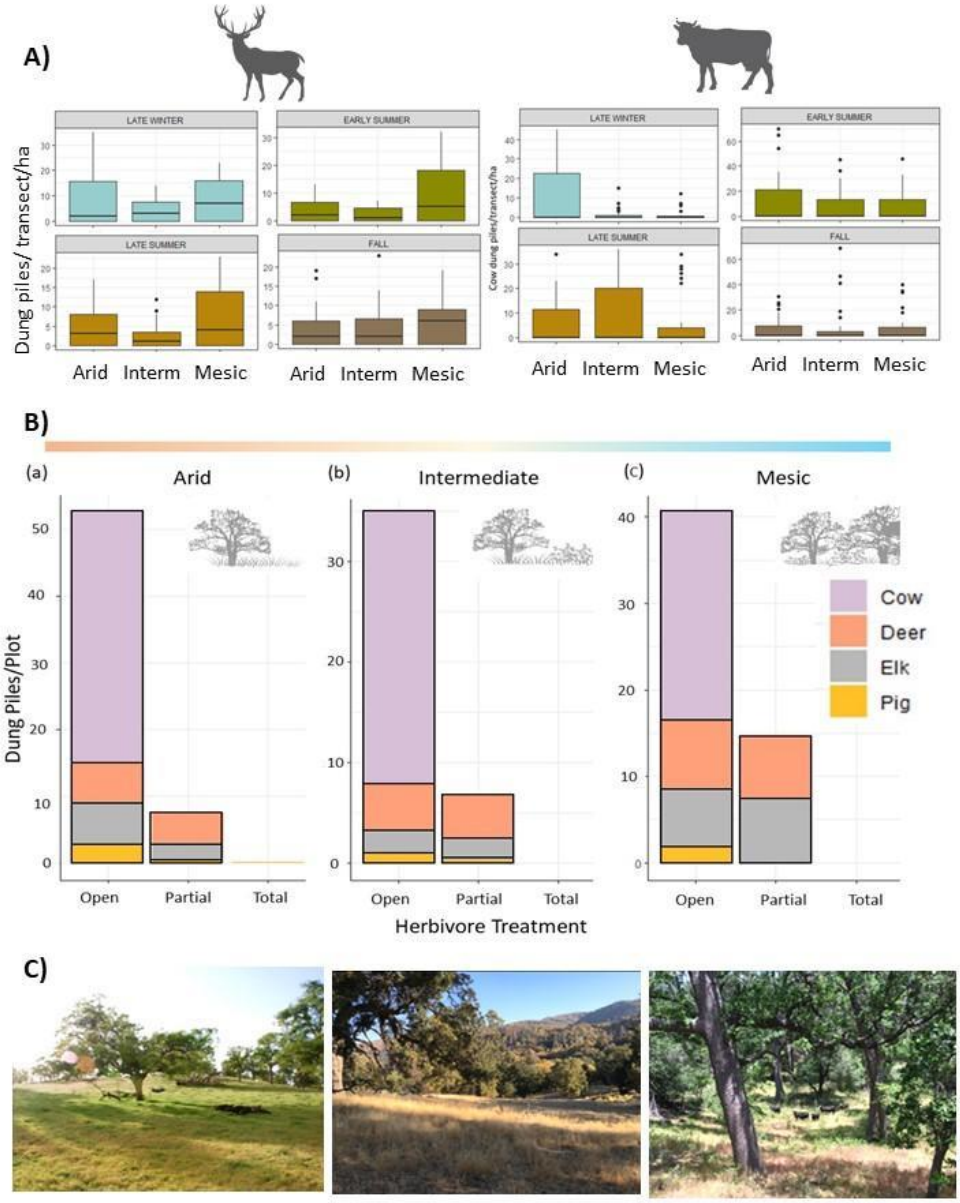

Figure 4: Herbivore activity across seasons, treatments, and climate levels

Counts of herbivore dung, a proxy for herbivore abundance, illustrate exclosures functioned as intended, and document activity patterns across experimental sites and seasons. A) Activity patterns of large herbivores across seasons and aridity levels (late winter in blue, early summer in green, late summer in tan, fall in brown) show slight seasonal shifts in wildlife activity and larger seasonal shifts in cattle activity (due to movement of cattle seasonally by land managers). B) Overall patterns in ungulate dung density across the three treatments and levels show that cattle are additive to wildlife. Deer and Elk were the two dominant wild ungulate species present. Bars are mean values for each species. Error bars have been omitted for clarity. C) Photos of open plots across the three aridity levels show the changes in vegetation associated with aridity.

2.4.2. 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, RDM, shading, and litter relative to partial and total exclosures (Figure 5). In these open plots, RDM, shading, and litter decreased with increasing aridity (Figure 5). These structural responses 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 more strongly modulated by aridity (Figure 5), and more likely to be weak or undetectable, relative to the effects of wildlife and cattle combined.

Aridity level on its own was not a significant predictor of cover, bare ground, or shading (Table 1); these structural metrics were consistent across the aridity gradient despite changes in species composition across the three levels (Figure 5; Appendix 1). Aridity level was an important predictor for RDM and litter volume (Table 1); this is expected, given that aridity and productivity covary in this system (Appendix 1). Despite being a poor independent predictor, aridity x treatment was significant for all structural metrics except for RDM (Table 1).

Plant cover was reduced in plots open to herbivory by wildlife and cattle relative to those with wildlife alone and full ungulate exclusion, and driven primarily by treatment and the interaction between treatment and aridity level (Table 1, Figure 5). Bare ground increased in the presence of wildlife and cattle at Intermediate and Mesic, but not Arid, and the overall difference was not significant (Figure 5). Wildlife alone had little effect except at Mesic, where bare ground appeared to increase slightly relative to total exclosures (Figure 5). The best predictors of bare ground were herbivore treatment and the interaction between treatment and aridity level (Table 1; Figure 5; $R^2m = 0.44$, $R^2c = 0.88$). RDM also increased inside exclosures across all three aridity levels; the final LMM of RDM included herbivore treatment and aridity level, but not their interaction (Table 1; Figure 5; $R^2m = 0.44$; $R^2c = 0.88$), demonstrating similar proportional offtake by herbivores across aridity levels and greatest offtake in open plots. Wildlife and cattle also substantially decreased shading (ΔPAR) relative to partial and total exclosures, while wildlife only decreased shading at Intermediate and had no effect on shading at Arid or Mesic (Table 1; Figure 5; $R^2m = 0.13$, $R^2c = 0.94$). Excluding herbivores increased shading by the understory vegetation regardless of the exclosure type (total or partial) or aridity level, and was best predicted by treatment and the interaction between treatment and level (Figure 5, Table 1). Similar to RDM and PAR, litter volume increased inside both partial and total exclosures, driven by treatment, aridity level, and the interaction between both predictors (Table 1, Figure 5; $R^2m = 0.84$, $R^2c = 0.87$).

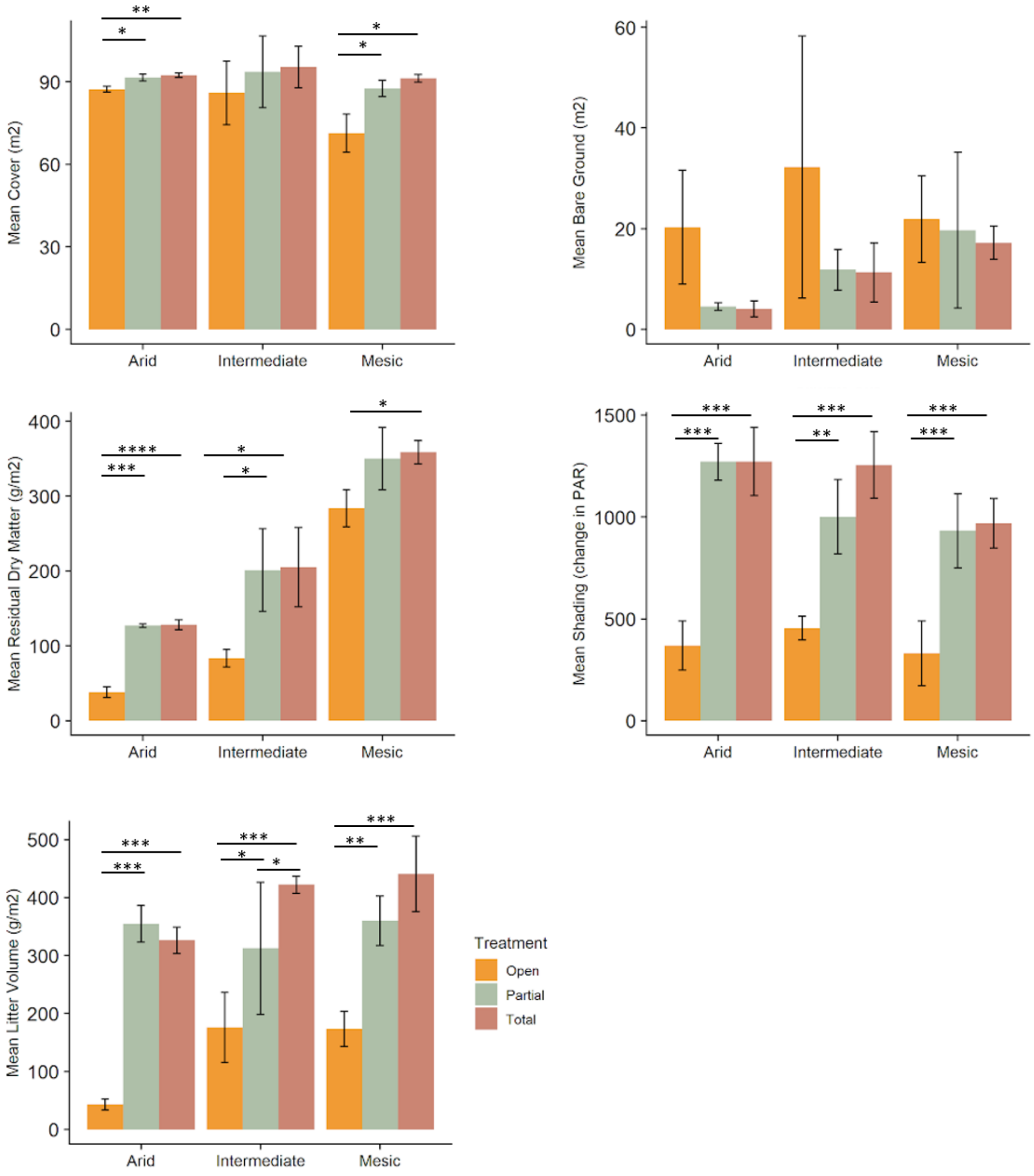

Figure 5: Herbivore treatments impact vegetation structure

Bar graphs (means,+/- SD) illustrating changes in structural metrics across treatments and climate levels. Overall, herbivores had strong effects on structure, with reductions in cover, RDM, shading, and litter when livestock and wildlife are present. Asterisk indicate significance levels (p <.05, p<.001, p<.0001, p<.00001).

2.4.3. 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 6). Across all aridity levels, wildlife had a neutral to positive effect on richness (Figure 6), while cattle with wildlife suppressed diversity at Mesic and enhanced it at Arid (Table 1; Figure 6). The final LMM for species richness included terms for herbivore treatment and the interaction between treatment and climate level (Table 1; Figure 5; $R^2m = 0.50$, $R^2c = 0.92$). On average, removing herbivores resulted in about four more species present inside exclosures than open control plots at Mesic, while herbivore presence increased richness by the same amount at Arid. At Intermediate, herbivores had no effect on richness (nor MPD or Shannon diversity).

Response variable	**Herbivore Treatment**		**Aridity Level**		**Treatment x Level**	
	***F*-value**	***p*- value**	***F*-value**	***p*- value**	***F*-value**	***p*-value**
Structural Metrics						
Total cover	**68.57**	**<.001**	0.80	.99	**9.97**	**<.001**
Biomass (g/m2)	**10.11**	**0.002**	**6.59**	**.008**	0.14	0.9642
Bare Substrate	**33.35**	**<.001**	0.31	.99	**14.91**	**<.001**
Litter volume	**292.83**	**<.001**	**30.85**	**<.001**	**7.578**	**<.001**
ΔPAR	**37.16**	**<.001**	1.82	0.191	**7.578**	**<.001**
Diversity Metrics						
Richness	**6.37**	**0.013**	2.22	0.1442	**7.6522**	**0.0027**
Shannon	**12.98**	**<0.001**	0.5418	0.591	**7.1233**	**.0035**
Berger-Parker	**11.10**	**.0007**	1.4316	0.2649	**3.8665**	**0.019**
MPD	**7.20**	**.012**	2.3744	0.6286	**4.1219**	**0.044**

Models included block nested within aridity level as a random effect. Bold values indicate a statistically significant difference.

Degrees of freedom = 2,18 for treatment; 2,18 for site; and 4,18 for treatment*site

Table 1: Mixed model results for analyses of herbivore impacts on plant communities

Results of the linear mixed model analyses for the effects of herbivore treatments and site aridity on plant community measurements.

Herbivore treatments generally had a similar impact on Shannon diversity as they had on species richness. The final LMM for Shannon diversity included terms for herbivore treatment and the interaction between treatment and climate level (Table 1; Figure 6; R^2m =0.41, R^2c = 0.86). The final model structure was similar for MPD (Table 1; Figure 6; R^2m = 0.54, R^2c = 0.63). Effects on MPD were slightly weaker, with significant differences only between open plots and total exclosures.

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 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 1).

2.4.4. Herbivore Exclusion Effects on Dominance

In contrast to diversity responses, dominance responses were nearly identical across herbivore treatments at both Intermediate and Mesic, and herbivores had no effect at Arid (Fig 6). Dominance was significantly higher within partial and total exclosures at Intermediate and Mesic than within open controls. The final LMM for dominance included terms for herbivore treatment and the interaction between treatment and level (Table 1; Figure 6; $R^2m = 0.59$; $R^2c = 0.67$).

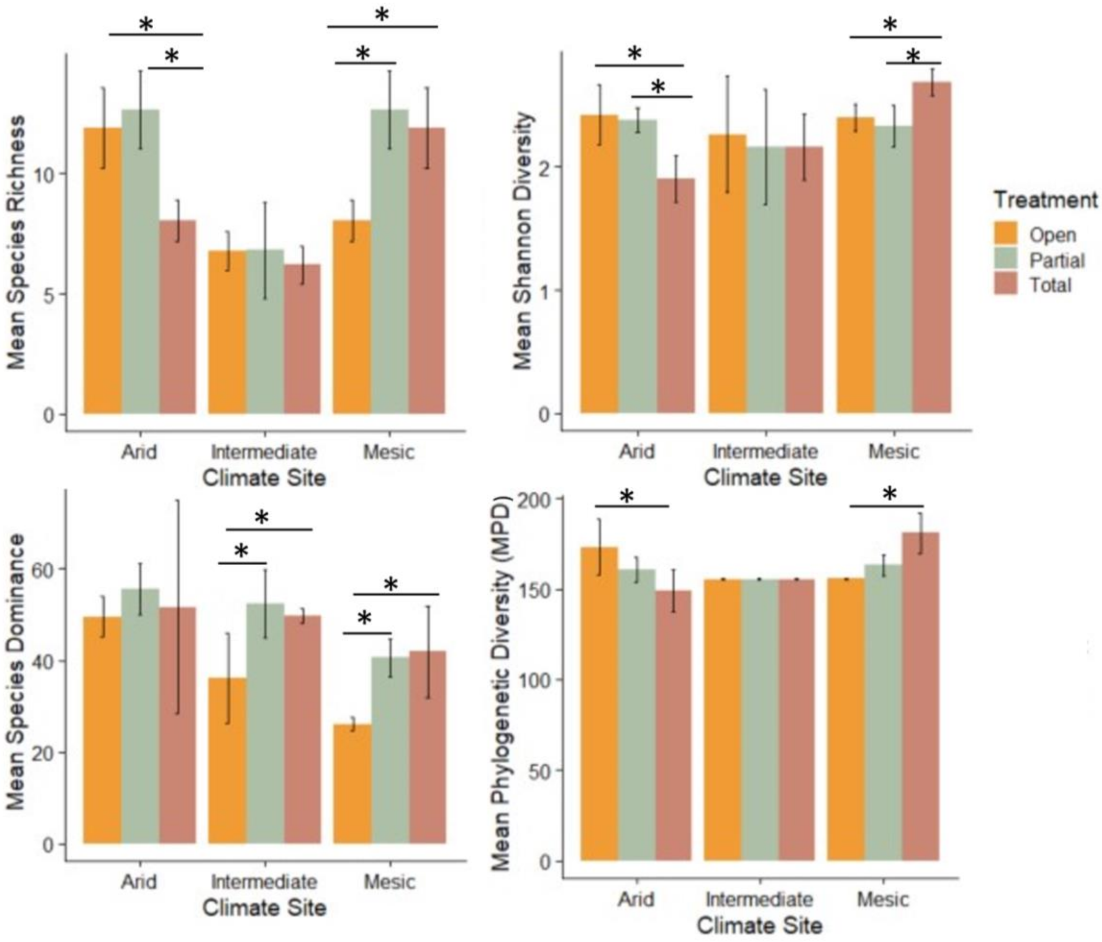

Figure 6. Effects of herbivores on plant species richness and diversity

Bar graphs (means,+/- SD) illustrating herbivore effects on richness and diversity. Herbivore treatment and aridity level impacted all diversity metrics investigated. Herbivore impacts were generally more distinct at high and low aridity, but not intermediate.. Asterisk indicate significance levels (p <.05, p<.001, p<.0001, p<.00001).

2.5. DISCUSSION

We found that the removal of large herbivores impacted both vegetation structure and plant community diversity. Climatic context only modulated the combined effects of wildlife and cattle on plant richness and diversity; effects on structural metrics and effects of wildlife did not vary with aridity. As expected, our results demonstrate 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. While our results support previous work, our study is the first to directly compare the functional consequences of common shifts in herbivore assemblages (wildlife loss, livestock addition) across varying climatic contexts within a single experiment.

Effects of herbivores on plant communities across the climate gradient

Consistent with other observations and experiments (Borer 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. Herbivores also increased bare ground at Intermediate and Mesic, but not Arid (Figure 5). These structural responses diverged between plots with both wildlife and cattle, and plots without cattle (Figure 5, Table 1). The independent effects of wildlife on vegetation structure were more strongly modulated by aridity (Figure 5), and more likely to be weak or undetectable, relative to the effects of wildlife and cattle combined. Arid blocks (the most arid of our three experimental levels) were located near the transition zone from savanna to grassland, and Mesic blocks (the least arid of our three experimental levels) 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 (for example, Goheen et al., 2013; Young et al., 2013). In contrast, when both livestock and wildlife are present, we find effects on cover, 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) to strongly negative effect (for richness, MPD, and Shannon diversity) 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, Perevolotsky, & Kigel, 2004) as well as from gradients at regional (Frank & Esper, 2005; H. S. Young et al., 2013), continental (Lezama et al., 2014) and intercontinental scales (Bakker et al., 2006; Milchunas & Lauenroth, 1993).

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, Nell, & Klinkhamer, 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, Mohamed Saleem, & Dibabe, 1997; Olff & Ritchie, 1998; Suominen, Niemelä, Martikainen, Niemelä, & Kojola, 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, Veblen, Goheen, Riginos, & Young, 2011; Odadi, Karachi, Abdulrazak, & Young, 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, Irby, & Pac, 1984). Ultimately, identity and density shifts are likely both extremely important, and interactively create either more heterogeneous or more homogenous 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.

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) are 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 belowground dynamics under arid conditions are not more important than aboveground 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 no change in dominance at Arid, and a decrease in dominance at Intermediate and Mesic (Figure 6). Despite this, richness was lower within total exclosure plots at Arid, and there was no effect on richness at Intermediate. Interestingly at Mesic, both dominance and diversity increased. We therefore did not find direct support for the dominance-richness hypothesis under any of these contexts. Yet, we also observed diversity responses that were completely inverted from those predicted by 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 turn, led to changes in palatability of dominant species 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.

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 nonnative 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, Smith, & Sykes, 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, Mittermeler, Mittermeler, Da Fonseca, & Kent, 2000).

Finally, it is also possible that the inverted 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 diversity within partial exclosures at Mesic that we observed. Shrubs such as *Ericamera* spp. have been shown to increase beta diversity and alter species richness patterns (Kleinhesselink, Magnoli, & Cushman, 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.

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, Elmore, Olander, Martin, & Harris, 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, while simultaneously 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, Snyder, Sloan, Zavaleta, & Fulfrost, 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.

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.

Further, 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 wildlife 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 also suggest that livestock and wildlife interact with climate in different ways. Again, the mechanism behind this difference is not entirely clear, but this difference suggests 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; Plas et al., 2016; Young, Okello, Kinyua, & Palmer, 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.

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Author Contributions:

DO and HY conceived the ideas and designed methodology; IM collected the climate data upon which this project was built and assisted with selection of the experiment's location; HY and DO received funding for this project; DO, AB, MK, ML, KK, CM, and BM collected data; DO analyzed the data; DO led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CHAPTER 2: APPENDIX 1

Appendix 1A– Description of Site Selection and Exclosure Design

Site selection: While we considered a number of locations in which to conduct this study, several conditions made Tejon a suitable case study both logistically and for producing generalizable results pertinent beyond the study site: (1) the Tejon Ranch Conservancy is supportive of this research and had a 10-year renewal permitting process, whereas public lands (e.g. Forest Service) had a 3-year permit cycle; the longer permit duration period was a better match for the infrastructure cost and long intended duration of the experiment; (2) plants (Franklin et al 2016), large mammals (Ratcliff et al 2018, Teton et al 2019), and climatic conditions (Davis and Sweet 2012, Dingman et al 2013; McCullough et al 2016) at the site are the subjects of prior studies and well documented; (3) the baseline ecology of this ecosystem is representative of oak-dominated systems throughout the region- including the majority of California's rangelands; (4) the wild mammalian herbivores are numerous and as diverse as anywhere in the state and representative of species widespread throughout western North America; (5) the plant community is composed of native and exotic species common throughout California and the western U.S., and (6) it's location along the southern edge of the San Joaquin Valley makes it particularly exposed to climate change, as it's near the southern range extent for many plant species, allowing access to a strong gradient in climate over short distances (8 km).

In the summer of 2015, we spent three months scouting potential sites prior to determining the final experimental location. Our study area had to be 1) within to the pre-existing downscaled climate grid (McCullough et al 2016), 2) of similar general vegetation: oak-dominated with a consistent understory of herbaceous vegetation, 3) of similar geologic parent material 4) accessible by 4wd vehicle (in order for movement and construction of fencing to be feasible), 5) on slopes <15%. Using mapping provided by the Tejon Ranch Conservancy and the Davis Lab UCSB, we identified a set of candidate sites that met these initial criteria. We then determined whether we could fit a full block (3 1ha plots) within each of those candidate sites; in many instances (~75% of sites that appeared suitable from satellite imagery and map layers) existing fencing, old roads, significant erosion, water troughs or salt blocks, ranching and hunting infrastructure, or other pre-existing disturbances made candidate sites non-viable after ground-truthing.

The remaining set of candidate sites were presented to the Ranch Company in January 2016. Final site selection was made by the Tejon Ranch Company (the landowner) to ensure that the experiment had no negative impact to Tejon's ranching or hunting activities, as well as to ensure that sites would be accessible by multiple entrance routes in case one road because washed out or otherwise unpassable, or in case of emergency (e.g. wildfire). This experiment was therefore located on a remote part of the ranch that receives very little visitation, thus minimizing the likelihood that human presence impacts wildlife or cattle movement. Ranchers were present at the sites only when actively moving cattle herds. Additionally, all experimental plots were situated within the boundaries of a single ranching lessee to avoid site differences due to different cattle management. Herd stocking density was approximately 0.13 cattle/ha (personal communication, April 2016).

Due to these logistical considerations, the final arrangement of blocks was concentrated onto three aridity "levels", yielding three replicate blocks per level (rather than 9 blocks spread along a gradient). These final levels were selected 1) to have a climatic difference of ~2C mean temperature and 200-300 mm annual (water year) CWD between each level (but minimal differences within a level), 2) to have similar slopes, aspect, and parent soil material within each level, 3) to allow three blocks within level, and three plots within each block, and 4) in close spatial proximity to reduce unintended sources of environmental variation. Within a level, blocks were 120 to 350 m apart.

Exclosure fencing construction: Fence construction began in September 2016 and was completed in November 2016. All twenty-seven plots were within 0.4 km of dirt access roads. Repairs following heavy rains and snow December 2016- February 2017 were made in March and April 2017, and repairs were made as needed throughout the experiment. Fences were regularly patrolled monthly (spring, summer, fall) to bimonthly (winter) to find and repair any breaks in the fence, with damage typically due to fallen trees, branches, or soil erosion during winter storms. Any large herbivores (or their signs) seen in the plots during these patrols were recorded as incidental observations and were removed through the access gate if inside an exclosure meant to keep them out.

In each plot enclosed by these barriers, there was a metal, hinged gate to allow entry to researchers. Total exclosure treatments were fully fenced using 2m high barbed wire fencing (wires 220 mm apart; the lowermost wire is smooth, to facilitate passage by small and medium-bodied wildlife (such as squirrels, rabbit), as well as carnivores (bobcat, coyote, mountain lion); partial exclosures use semi-permeable barriers made of 1.07 m high barbed wire spaced 300 mm apart and connected to short metal T-posts (this construction is the same as all fences across the ranch used to limit cattle movement while enabling passage by wild ungulates that can readily jump over or crawl under the barriers). Open plots are fully permeable and completely unfenced, with 1 m high t-posts demarcating plot boundaries. While it would be ideal to have a fully factorial design, a treatment that excluded wild ungulates but was open to cattle was not feasible given free-roaming cattle in this system and the additional burden on ranchers to actively move cattle in and out of plots was not practical here. The central 0.25 ha of each plot was used for short-visit, descriptive data collection (e.g. composition surveys); more manipulative activities (biomass clipping, soil sampling) were restricted to the plot edges. The 1ha plot size allowed us to minimize edge effects and granted more confidence in the observed patterns.

To ensure plot locations accurately captured measured and modeled CWD, blocks were situated either adjacent to or within 500 m of a weather station used by McCullough et al (2016). CWD, calculated as potential evapotranspiration minus actual evapotranspiration, can be thought of as a surrogate for plant water demand in a Mediterranean climate: changes in CWD effectively quantify the supplemental amount of water needed to maintain current water balance given projected increases in air temperature and evaporative demand, and CWD is a good predictor of plant distributions (Anderegg et al., 2015; Lutz, Wagtendonk, & Franklin, 2010; Stephenson, 1990). While MAP (mean annual precipitation) is a commonly used proxy for productivity in many systems, other factors such as solar radiation, slope and aspect may be equally if not more important in driving plant production, especially in California's topographically heterogeneous landscapes (Bartolome et al., 2007), with significant impacts on plant community diversity and composition (Olff & Ritchie, 1998; Osem et al., 2002). CWD helps account for this by spanning climate-mediated variation in soil fertility, soil water holding capacity, and slope and aspect variation (Figure 2) over a relatively small (8.5 km) spatial scale.

These sites also roughly represent present, future, and far-future climate scenarios. Estimates of future scenarios are based on projections (McCullough et al., 2016) which predict upslope migration of drought-tolerant oak species, particularly *Q. douglasii*, and declines in *Q. kelloggii* in response to net increases in aridity. These predictions are consistent with both recent historical trends and dynamic vegetation models (Kelly & Goulden, 2008; Lenihan, Bacheler, Neilson, & Drapek, 2008; McIntyre et al., 2015), indicating that more mesic areas are likely to transition toward communities currently present downslope (Kelly & Goulden, 2008; Lenihan, Bacheler, Neilson, & Drapek, 2008; McIntyre et al., 2015). While rarely, if ever, is there enough information to predict with certainty how species assemblages will shift with climate change, our experimental sites represent one plausible data-driven scenario of future trajectories in this system, and are therefore useful both for understanding present heterogeneity as well as predicting future change.

Appendix 1B– Establishing a Relationship Between Aridity and Productivity

To determine whether our three aridity levels also correspond to different levels of primary productivity—thus enabling us to consider our work in the context of prior research on herbivore effects on richness-productivity relationships—we established that aridity and productivity covary in our system. We used three proxies for primary productivity (Fig 2). First, we extracted the Normalized Difference Vegetation Index (NDVI) for each climate level using the USGS Modis satellite image database (https://lpdaac.usgs.gov/tools/usgs-earthexplorer/), and recorded the 5-year (2010-2015) maximum NDVI values of each block (taken prior to exclosure installation, n = 9 satellite NDVI value grids per level). Second, we collected aboveground standing biomass from 5 haphazardly selected (subject to their having continuous understory vegetation and no tree basal area) .5m^2 quadrats per plot in June 2016 prior to exclosure installation. Biomass was clipped at the soil surface, bagged, dried for 48 hr at 38 ºC, and weighed (n = 15 quadrats per block, 45 per level). Third, in July 2016, we estimated standing biomass using a modified point-intercept method (Robel et al

1970, Frank and McNaughton 1990): using three 50m transects established in the inner .25ha of each plot, we recorded total hits along a 5-point pin frame (n = 300 pin drops per plot).

For each metric, we investigated whether the three levels differed significantly using ANOVA for NDVI and Kruskal-Wallis Tests for pin hits and biomass in R. Mean max NDVI was significantly different among the three levels ($F_{2,24} = 630.5$, $P = <.001$), with lowest values at Arid and highest at Mesic. Pin hit data were significantly different between Arid and the other two levels, but not between Intermediate and Mesic ($\chi^2 = 0.92114$, df = 2, $P < .001$). Aboveground biomass was significant different across all levels ($\chi^2 = 86.161$, df = 2, $P < .001$), again, with greatest aboveground standing biomass at Mesic and least at Arid.

Overall, all three measures showed the same trend, with productivity proxies mostly increasing from Arid to Mesic, supporting variation in productivity across our three sites paralleling changes in CWD. We therefore consider the three categorical climate levels (Arid, Intermediate, Mesic) as also representative of distinct primary productivity levels (low, medium, high) and reference literature on both climate and productivity when discussing our experiment and results.

Appendix 1C– Examining Soil Properties

To assess whether soil properties differed across experimental units, we collected 15-cm deep soil cores every 10 m along two transects paralleling the periphery of the central .25ha of each plot. Samples from each plot were dried (60 C for 72 hours), homogenized into one sample per transect (n=2 per plot), and sieved through 2-mm mesh, and sent to Brookside Laboratories (New Knoxville, OH) for analysis of pH, organic matter (derived from loss on ignition), NH_4-N, NO_3-N, K, P, Fe, Na, and total exchange capacity (TEC). Gravimetric water content, measured as the difference between the wet weight and dry weight of soils, was collected for a subset of samples (n=18). We investigated whether the three levels differed significantly for each metric using MANOVA.

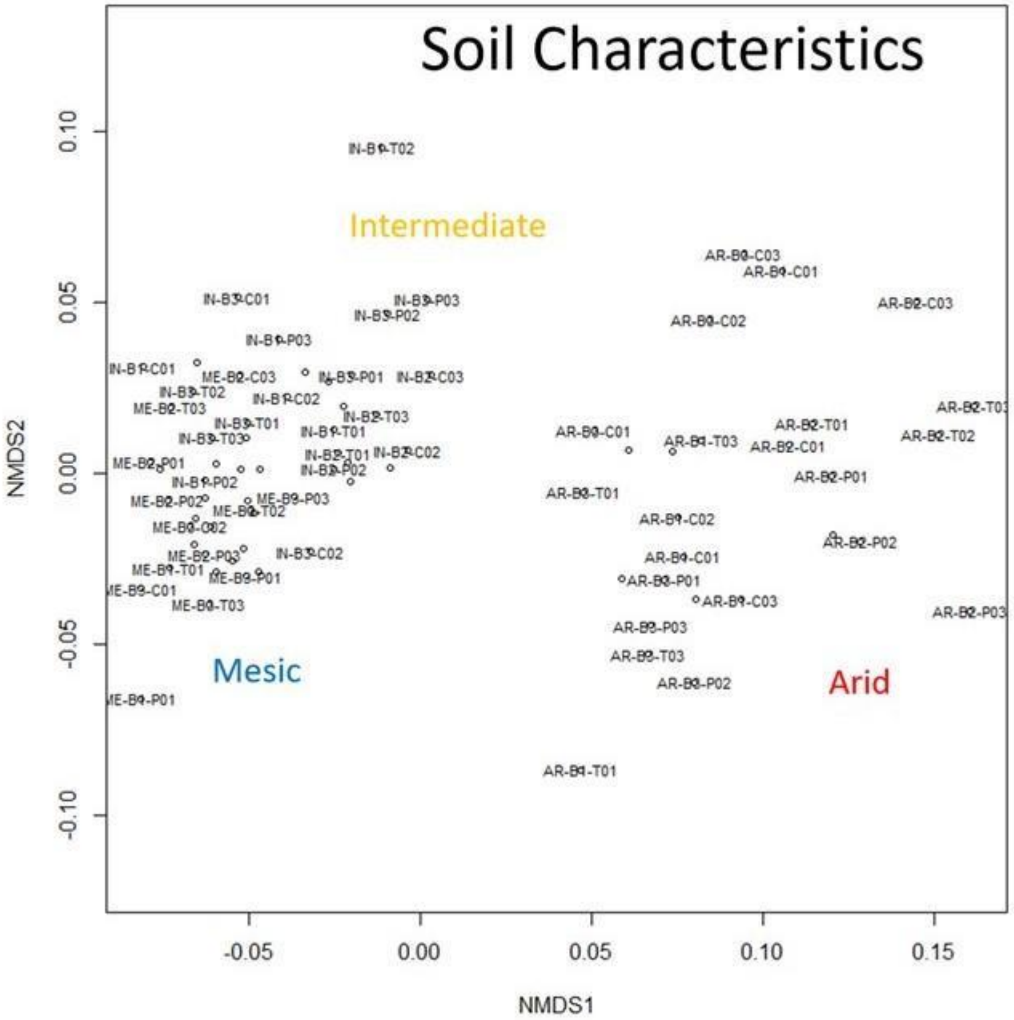
Total exchange capacity (TEC), gravimetric water content (GWC), organic matter, NH_4-N, NO_3-N, P, and Fe were significantly different among climate levels, with mesic sites generally exhibiting higher resource availability, a pattern consistent with expectations of climate-mediated resource variation (one-way ANOVA, $p < 0.001$; Table 1 and 2). There was no significant difference in pH, Na, or K.

Level	Organic matter	Gravimetric water content (GWC)	Total exchange capacity (TEC)	pH	NH_4	NO_3	P	K	Fe	Na
Arid	14.334	0.185	15.202	7.13	12.12	12.20	59.00	445.28	105.17	24.28
Interm	6.517	0.25	18.537	7.17	15.74	18.76	102.72	555.11	160.50	24.94
Mesic	11.001	0.456	21.625	7.06	26.87	27.44	156.78	551.78	171.50	24.83

Appendix 1, Table 1. Mean values of soil properties measured per aridity level.

Soil Property	**Aridity Level**	
	***F* value** (df =2, 51)	**Pr(> *F*)**
Organic matter	**35.02**	**<.001**
GWC	**13.95**	**<.001**
TEC	**21.14**	**<.001**
pH	.396	.675
NH4	**16.41**	**<.001**
NO3	**10.55**	**.0001**
Na	.301	0.741
P	**54.08**	**<.001**
K	1.127	.332
Fe	**57.29**	**<.001**

Appendix 1, Table 2. Significant differences in soil properties across the three levels reflect differences we would expect due to climate variation. There were no significant differences in pH, sodium, or potassium.



Appendix 21, Figure 1. NMDS ordination of soil samples by aridity level. The distance between points represents Bray-Curtis dissimilarity. Mesic and Intermediate soils appear more homogeneous (clustered most strongly) than Arid soils. Mesic and Intermediate soils also appear more similar to each other than to Arid, likely reflecting the geographic spread of sites (Mesic and Intermediate blocks were geographically closer, approx. .6 km apart, than either was to Arid, approx. 8 km).

Appendix 1D- Variation in Tree Canopy Cover Across Experimental Plots

Climate Level	Block	Treatment	% Canopy Cover
Arid	1	Control	21.115
Arid	1	Partial	24.017
Arid	1	Full	24.431
Arid	2	Control	15.820
Arid	2	Partial	21.006
Arid	2	Full	35.503
Arid	3	Control	52.572
Arid	3	Partial	30.552
Arid	3	Full	22.608
Intermediate	1	Control	18.736
Intermediate	1	Partial	37.699
Intermediate	1	Full	20.418
Intermediate	2	Control	50.641
Intermediate	2	Partial	33.349
Intermediate	2	Full	41.772
Intermediate	3	Control	44.117
Intermediate	3	Partial	44.275
Intermediate	3	Full	34.368
Mesic	1	Control	57.818
Mesic	1	Partial	59.721
Mesic	1	Full	50.778
Mesic	2	Control	53.937
Mesic	2	Partial	35.727
Mesic	2	Full	45.467
Mesic	3	Control	33.047
Mesic	3	Partial	33.467
Mesic	3	Full	33.947

Appendix 1, Table 3. Estimated percent canopy cover for each experimental block.We estimated tree canopy cover using the program ImageJ (Shneider et al 2012) to calculate canopy area from aerial satellite imagery of each plot (Google Earth) collected between 2007 and 2015.

1. Schneider, C.A., Rasband, W.S., Eliceiri, K.W. "NIH Image to ImageJ: 25 years of image analysis". Nature Methods 9, 671-675, 2012.

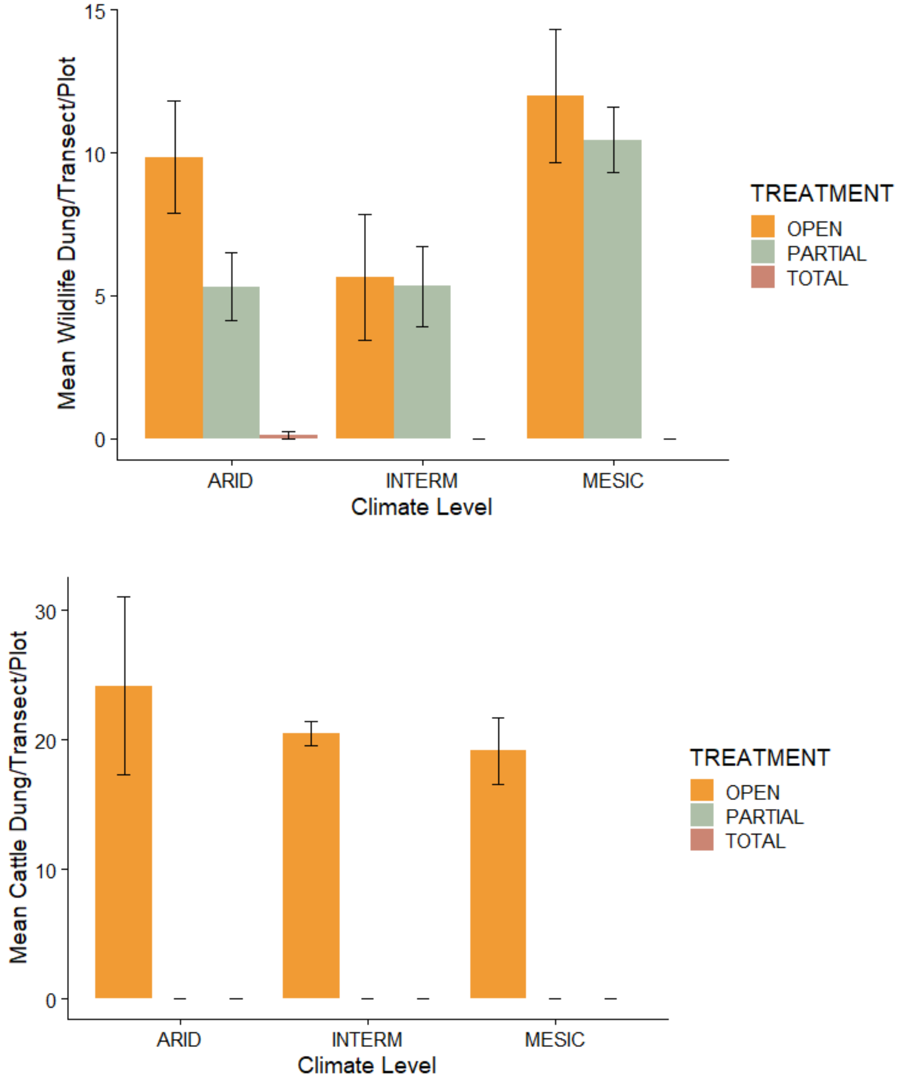
Appendix 1E- Monitoring Large Herbivore Activity

An overview of dung patterns is presented in the main text. Here, we describe the dung count analyses and results, as well as differences in activity among individual wildlife species.

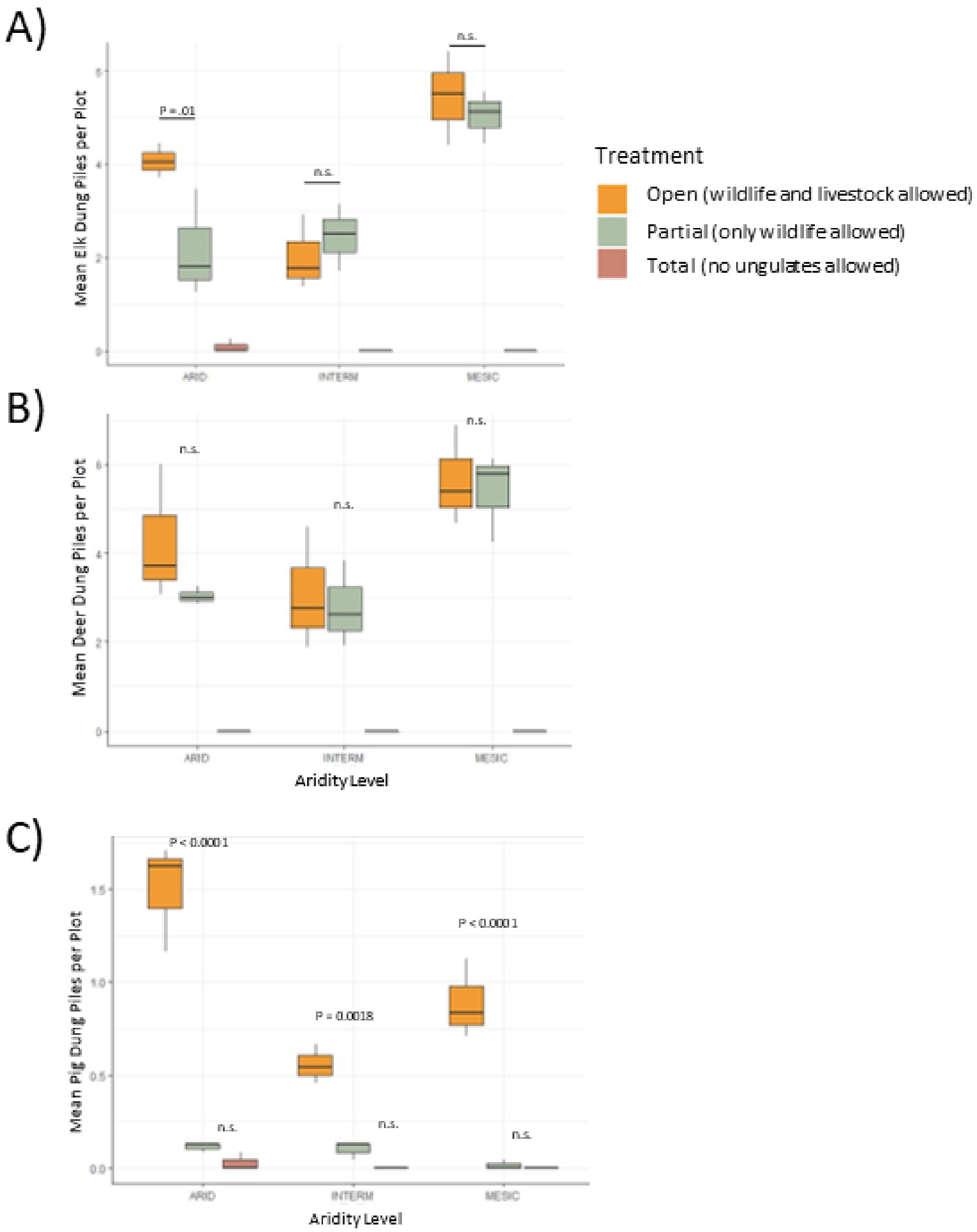
Wildlife dung: We used generalized mixed models with a poisson distribution for wildlife dung patterns. Models included treatment (n=3), climate level (n = 3), year (n=2), and their interactions as fixed effects, and block (n=9) and transect (n = 4/plot) as nested random effects (Zuur et al. 2009). We built all models in the lme4 package in R (R version 3.5.0, lme4 v 1.1-17, Bates et al. 2015). We selected the best fitting model by minimizing AICc values (MuMIn package v 1.42.1, (Burnham & Anderson 2002) and generated p-values of the final models using parametric bootstrapping with 10,000 iterations (pbkrtest package v 0.4-7, Halekoh & Hojsgaard 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 examined pairwise differences using Tukey's Honestly Significant Difference (HSD) post-hoc tests (package emmeans). Significant effects of level in these models reflect variation in activity levels across the aridity gradient. Significant effects of treatment reflect variation in activity levels across treatment types.

GLMM results indicate that treatments were effective at excluding target wildlife from total exclosures, but may have either had the unintended effect of reducing activity within partial exclosures as well, or else wildlife preferentially selected sites that had been previously grazed by cattle. There was a significant difference ($p <.001$) among all three treatment types in wildlife dung abundance. Activity appears bimodal, with highest activity levels at Mesic and Arid, but significantly lower activity at Intermediate ($p <.01$). Our best fit model for wildlife activity included treatment, climate level, their interaction with year ($R^2m = 0.997$, $R^2c =0.9998$; AICc = 3222; ΔAICc = 94) and both random effects terms, though upon further investigation, there was not a significant overall difference between herbivore activity in 2017 and 2018 ($p = 0.153$).

Cattle dung: Because visual inspection of the data showed exclosures clearly functioned as intended for removing cattle from partial and total exclosures (S3-Figure 1b), we investigated effects of level, year, and their interaction on cattle dung abundance for open plots only. Our best fit model for cattle dung included climate level, year, and their interaction ($R^2m = 0.003$, $R^2c =0.826$; AICc = 2740 ; ΔAICc = 30). Cattle dung was significantly different ($p <.001$) at Arid relative to Intermediate and Mesic, and dung abundance differed across all sites between 2017 and 2018, suggesting there was a change of some kind in management over that period.



Appendix 1, Figure 2. Summary graphs for dung counts (mean and standard deviation) for all wildlife (top) and cattle (bottom). There was a significant difference in dung abundance across treatment types, indicating that treatments operated successfully and kept intended herbivore groups from entering. However, there was a slight decrease in wildlife activity in partial exclosures vs. open plots at Arid ($p < 0.05$), indicating that fencing may have unintentionally deterred some wildlife.



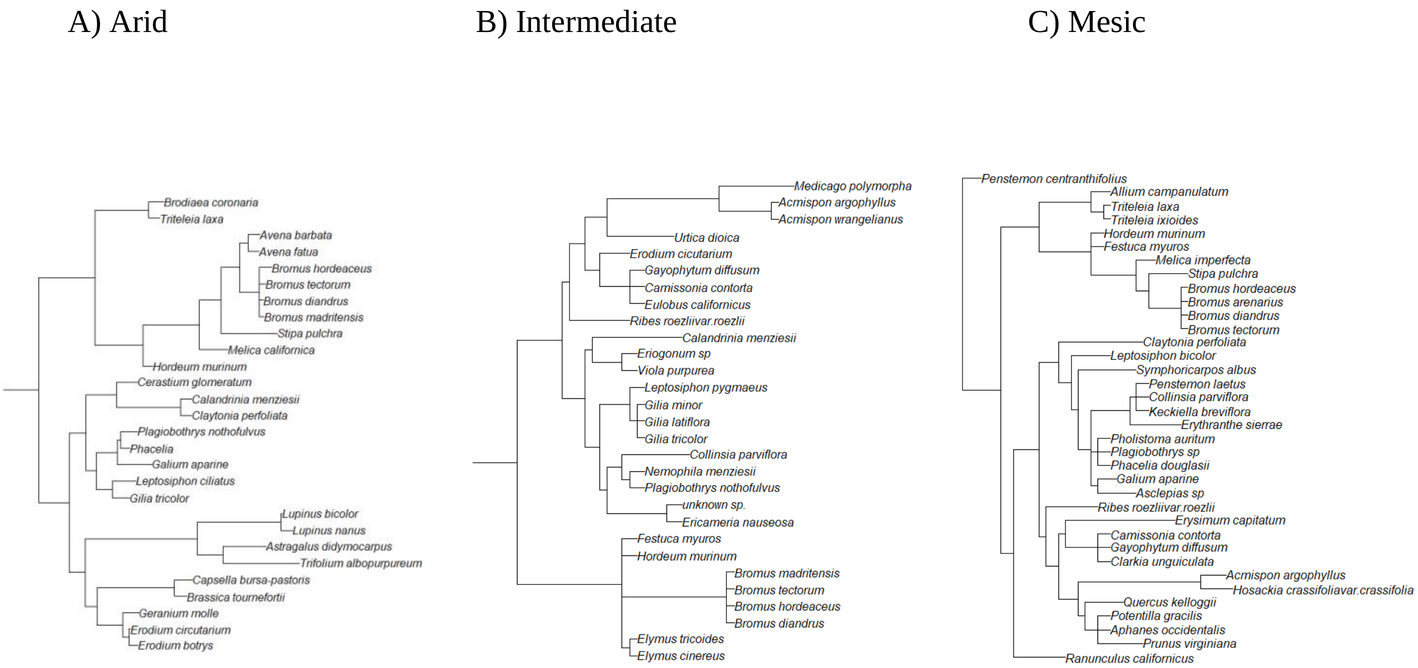
Appendix 1, Figure 3. Activity (dung counts) of wildlife species varied by plot and aridity level. Elk and pig were more active in open than partial exclosures at Arid; pig were more active in open plots at all sites.

Appendix 1F- *Plant Species Composition*

To understand which species could be driving diversity changes, we examined rank abundance curves (vegan package), and used the package mvabund (Wang et al 2012) to examine differences in species composition, fitting generalized linear models with a negative binomial distribution to each species and then used resampling to test for significant community level and species level responses. This is an alternative approach to perMANOVA that better handles a wider range of multivariate data and is not based on distance matrices, allowing for easier interpretation of results. Because our intention was not to examine changes in community composition across climate levels (as species assemblages differ, with high species turnover across sites), we modeled each of the three sites separately for composition analyses.

We found that plant community composition differed across treatments at Arid (LRT = $230_{2,6}$, $p < 0.01$), and Mesic ($207_{2,6}$, $p= 0.011$), but did not differ significantly across treatments at Intermediate (LRT = $60.34_{2,6}$; $p = 0.152$). Composition varied significantly by block at two levels (interm: LRT = $80_{2,6}$, $p = 0.043$, mesic: LRT = $116_{2,6}$; $p = .01$), but not at arid ($22.78_{2,6}$; $p = 0.685$). At Arid, the community was dominated by *Bromus diandrus* and *Bromus hordeaceus,* two invasive annual grasses; at intermediate, *Bromus diandrus* and *Ericamera nauseosa*, a native woody shrub; and at mesic, the two most abundant species were *Ribes roezlii*, a thorny native shrub, and *Galium aparine*, an annual native forb. At Arid, these shifts were driven by significant changes in abundance of 2 grasses, *Bromus diandrus* ($p= 0.017$) and *Bromus hordeaceus* ($p=0.049$), which increased within total exclosures and partial exclosures, and one forb, *Acmispon wrangelianus* ($p= 0.051$) which was marginally more abundant in open plots. Several species were detected only inside exclosures—*Lupinus nanus, Triteleia laxa*—while several others were never or rarely detected within either exclosure type (*Leptosiphon spp. Broidea coronata)*. At Intermediate, though there was not a significant overall treatment effect, we did observe a trend towards increasing *B. diandrus* cover inside exclosures relative to open plots. At Mesic, there were significant changes in abundance of 4 forbs: *Keckiella breviflora* (p= 0.003), *Galium aparine* (p= 0.005), *Collinsia parviflora* (p= 0.039), increased inside partial and total exclosures, while *Ranunculus californicus* (p= 0.005) was substantially more abundant in open plots.

1. Wang, Y. I., Naumann, U., Wright, S. T., & Warton, D. I. (2012). mvabund–an R package for model-based analysis of multivariate abundance data. Methods in Ecology and Evolution, 3(3), 471-474.



Appendix 1, Figure 4. Phylogenetic trees and plant species lists for the communities sampled across the three aridity levels (Arid, Intermediate, Mesic).

Phylogeny construction: We used all species from vegetation surveys to create a phylogenetic tree using the Phylomatic tool, version 3 (http://phylodiversity.net/phylomatic/) (Webb & Donoghue, 2005) and based on the APG III (2009) phylogeny. If species were not available in the tree, we used genus-level classification. We then used Phylocom 4.2 to add branch lengths to the phylogeny (Gastauer & Meira-Neto, 2013).

Appendix 1G- Change in Exotic species richness and diversity

To better understand the role of exotic species in observed richness and diversity patterns, we conducted a follow-up analysis for exotic species only. We followed similar linear mixed effect model procedures to those previously described for the response variables exotic species richness and exotic species Shannon diversity. Our best fit model for exotic species richness included climate level, herbivore treatment, and their interaction (exotic richness: R^2m = 00.5165, R^2c =0.7345; AICc = 2740 ; ΔAICc = 11.315). Our best fit model for exotic Shannon diversity also included climate level, herbivore treatment, and their interaction (exotic richness: R^2m = 0.8587, R^2c = 0.927; ΔAICc = -1019.8351).

```
                Df      Sum Sq         Mean Sq       F value          Pr(>F)
Treatment    2              36              18.236          3.388            0.0342 *
Residuals   969     5215             5.382
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

```
                        Df      Sum Sq         Mean Sq       F value          Pr(>F)
Aridity Level    2          3378             1689.2          873.9           <0.0001 ***
Residuals   969     1873             1.9
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Appendix 1, Table 4 ANOVA results of 1) herbivore treatment effect on richness of exotic species and 2) differences in exotic species richness across aridity levels.

Level = Arid:

```
contrast               estimate      SE     df     t.ratio  p.value
Open - Partial    0.5278        0.184 957     2.871  0.0117 *
Open - Total      1.0370        0.184 957     5.641  <.0001 ***
Partial - Total   0.5093        0.184 957     2.770  0.0158 *
```

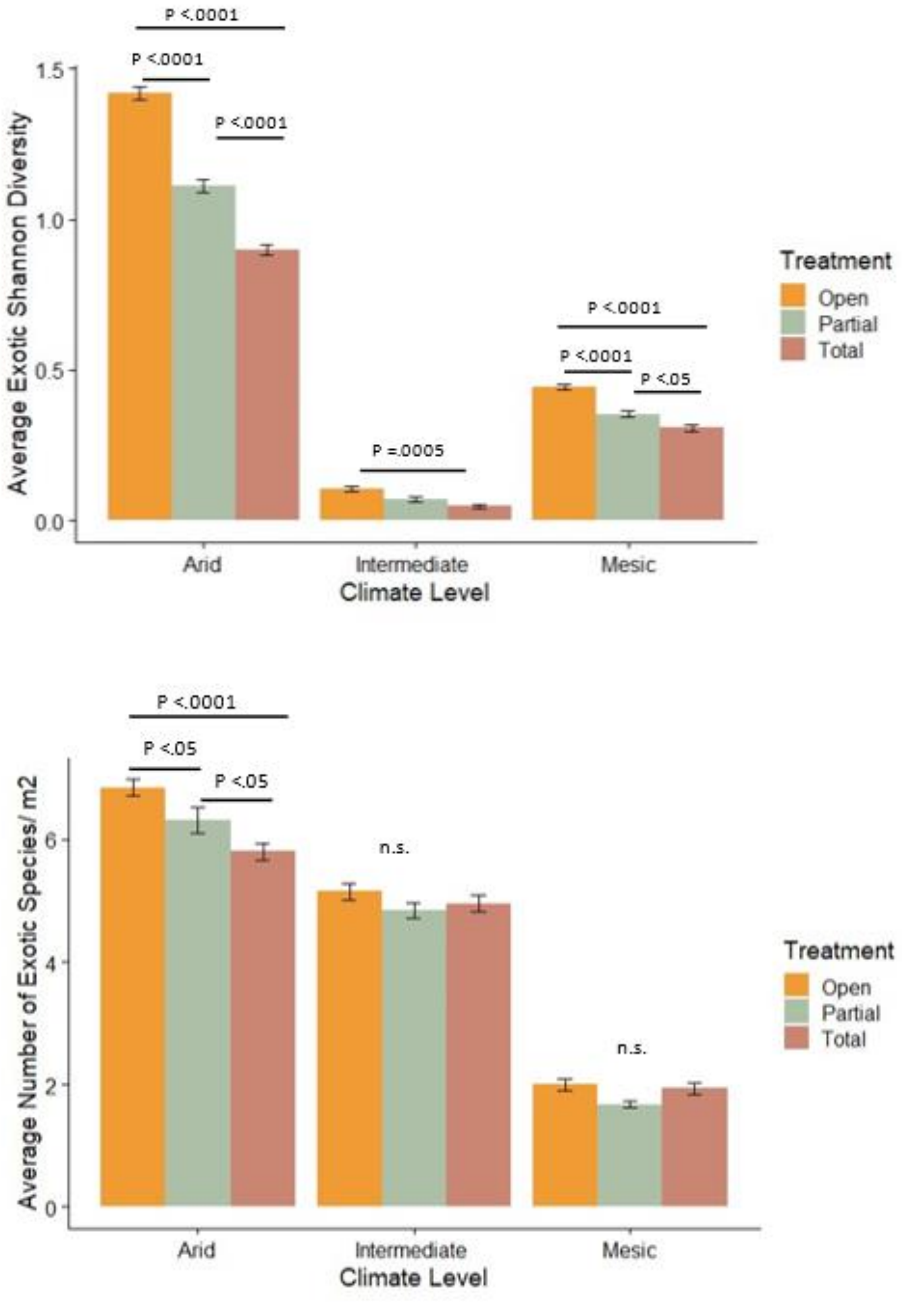
Level = Intermediate :

```
contrast                estimate      SE     df      t.ratio p.value
Open - Partial     0.3056        0.184 957     1.662  0.2205
Open - Total            0.1944   0.184 957     1.058  0.5407
Partial - Total        -0.1111   0.184 957    -0.604  0.8178
```

Level = Mesic:

```
contrast                estimate      SE    df      t.ratio p.value
Open - Partial     0.3241        0.184 957     1.763  0.1828
Open - Total       0.0645        0.184 957     0.351  0.9343
Partial - Total   -0.2595        0.184 957    -1.412  0.3353
```

Appendix 1, Table 5. Results of fixed effects tests from mixed models testing for differences in exotic species richness across treatments and aridity levels. When there were significant main effects, we used Tukey’s multiple comparisons to test for differences among treatments within levels, with degrees of freedom calculated following the Kenward-roger method.



Appendix 1, Figure 5. Summary graphs for exotic species richness (top) and exotic species Shannon diversity (bottom). There were significant treatment differences at Arid, but not Intermediate or Mesic. However, there were treatment effects at all levels for Shannon diversity.

Effect of Herbivore Treatment

```
                 Df Sum Sq Mean Sq F value   Pr(>F)

Treatment         2   9.24   4.619   20.07 2.88e-09 ***

Residuals       968 222.74   0.230
```

Effect of Aridity Level (Site)

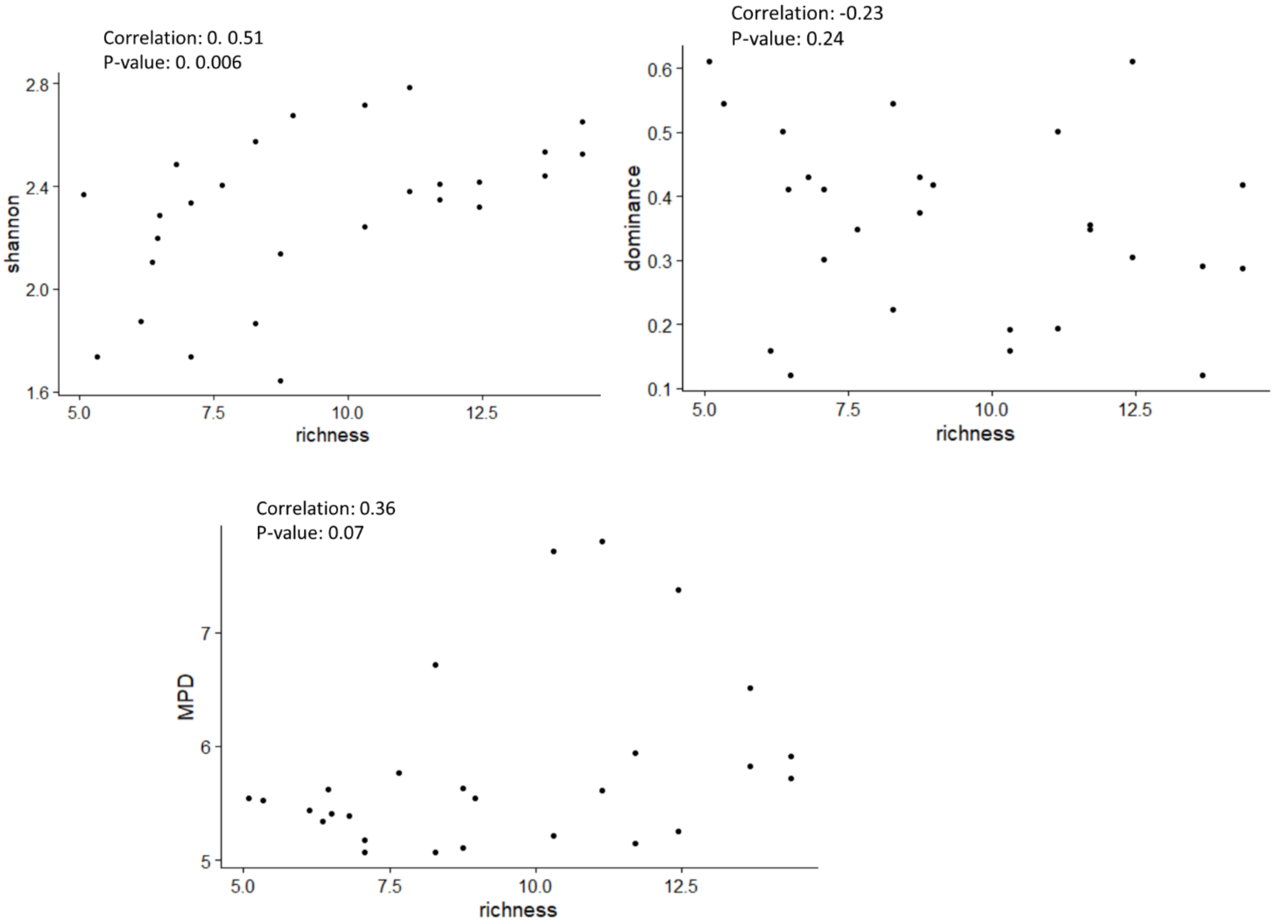
```
            Df   Sum Sq Mean Sq F value Pr(>F)

Level        2   196.42   98.21    2673 <2e-16 ***

Residuals  968    35.57    0.04
```

Table A1-6. ANOVA results of 1) herbivore treatment effect and 2) aridity level on Shannon diversity exotic species.

```
Level = Arid:
 contrast                  estimate    SE     df       t.ratio p.value
 Open - Partial    0.3059  0.0186 956 16.484  <.0001 ***
 Open - Total      0.5193  0.0186 956 27.981  <.0001 ***
 Partial - Total   0.2133  0.0186 956 11.496  <.0001 ***

Level = Intermediate :
 contrast                       estimate    SE  df t.ratio p.value
 Open - Partial     0.0332  0.0186 956  1.783  0.1758
 Open - Total       0.0583  0.0186 956  3.140  0.0050 **
 Partial - Total    0.0251  0.0186 956  1.349  0.3682

Level = Mesic:
 contrast                 estimate    SE  df t.ratio p.value
 Open - Partial    0.0881  0.0186 956  4.747  <.0001 ***
 Open - Total      0.1347  0.0186 956  7.258  <.0001 ***
 Partial - Total   0.0466  0.0186 956  2.512  0.0326 *

Degrees-of-freedom method: kenward-roger
P value adjustment: tukey method for comparing a family of 3 estimates
```

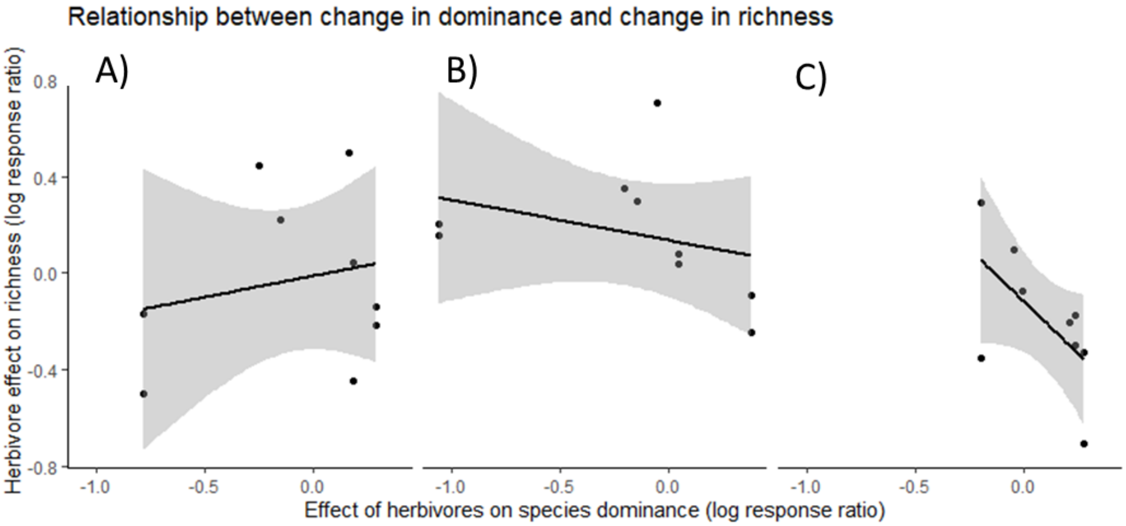
Table A1-7. Results of fixed effects tests from mixed models testing for differences in exotic species shannon diversity across treatments and aridity levels. When there were significant main effects, we used Tukey’s multiple comparisons to test for differences among treatments within levels, with degrees of freedom calculated following the Kenward-roger method.

Appendix 1G **-** *Correlation among diversity metrics*



Appendix 1, Figure 6. Pearson’s correlation among (top left) richness and Shannon diversity; (top right) richness and dominance; (bottom left) richness and MPD. Richness and Shannon diversity were significantly positively correlated; richness and dominance were negatively correlated, but not significantly so; and richness and MPD were positively correlated, but not the relationship was not significant.

Appendix 1H- Dominance effect size and relationship with species richness



Appendix 1, Fig 7. Linear models exploring the relationship between dominance and richness across (A) all herbivores [ln(full exclosure/open access area)], (B) large herbivores only [ln(partial exclosure/open access area)], or (C) small herbivores [ln(full exclosure/partial exclosure)] on plant species richness. The shaded area shows the 95% confidence interval of the predicted relationship around the regression line. None of the effect size relationships were significant ($p > 0.05$).

CHAPTER 3: EFFECTS WILD AND DOMESTIC HERBIVORES ON TICK SURVIVORSHIP

Publication Note: The content of this chapter is under review for publication in “Effects of wild and domestic herbivores on tick survivorship.” Orr *et al.*, *Journal of Applied Ecology,* Copyright © 2021, Wiley-Blackwell

3.1 ABSTRACT

1. The management of large-bodied mammalian hosts for control of ticks and tick-borne infectious disease has yielded mixed success. Large-bodied mammals—especially ungulates— as hosts for adult ticks, play an important role in maintaining tick-borne disease cycles. However, they can also affect tick disease cycles indirectly, including by altering microclimates important for tick survivorship through grazing and trampling of vegetation. These indirect effects may be more important than previously recognized for tick survivorship and can influence host seeking behavior, tick abundance, and human exposure risk.

2. Here, we use a large-scale field experiment in California to investigate the effects of ungulate management on survivorship rates of two common tick species, *Ixodes pacificus* and *Dermacentor variabilis*. Specifically, we employ an *in situ* larval tick survivorship experiment to isolate the indirect effects of ungulate management on tick survivorship rates and explore how these effects vary across climatic contexts. We then examine the extent to which any survivorship changes are mechanistically explained by changes in vegetation density and microclimate.

3. We find ungulate management dramatically changes larval tick survivorship of both tick species, but that the effect varies across climatic contexts. In arid and intermediate contexts, total ungulate removal increases tick survivorship while cattle presence reduces survival. Conversely, under cooler, wetter conditions, both presence of cattle and complete ungulate removal increase tick survivorship. Our results strongly suggest that ungulate herbivores impact larval survivorship through their indirect effects on microclimate. Effects are likely stronger under more arid contexts because microclimate suitability plays a more prominent role in limiting survivorship times in these desiccating environments.

4. *Synthesis and applications*. We provide experimental evidence to demonstrate that increasing abundance of ungulates, both wild and domestic, can reduce larval tick survivorship, likely truncating host-seeking activity and with strong potential effects on disease transmission, as larval *survival* to the nymphal stage is the critical parameter affecting TBD risk. Especially in drier environments, management of ungulate herbivores and targeted grazing to reduce understory vegetation may be an effective landscape intervention strategy for disease risk mitigation.

3.2 INTRODUCTION

Anthropogenic global change is profoundly impacting species and ecological processes of concern to human health, including accelerating emergence and transmission of vector-borne disease (Gray, Dautel, Estrada-Peña, Kahl, & Lindgren, 2009; MacDonald & Mordecai, 2019; Nick H. Ogden, Mechai, & Margos, 2013). Over half the world's human populations are currently at risk from vector-borne infections (CDC, 2014), and ticks are one of the top vectors of human disease (De La Fuente, Estrada-Pena, Venzal, Kocan, & Sonenshine, 2008; Swei, Couper, Coffey, Kapan, & Bennett, 2020). Tick-borne diseases

(TBDs) are increasing globally, apparently as a result of human perturbation of natural systems (Allan, Keesing, & Ostfeld, 2003; Eisen, Kugeler, Eisen, Beard, & Paddock, 2017; McMahon, Morand, & Gray, 2018). Unfortunately, many TBDs are difficult to diagnose, and often affect people in regions where medical access is limited (Sokolow et al., 2019). Therefore, prevention—via tick checks, proper clothing and acaricide use, and reduction of infected vectors in the landscape—has been identified as the most effective approach for reducing the burden of TBDs (CDC, 2020).

One commonly suggested ecological TBD prevention strategy (particularly on the east coast of North America, Perkins, Cattadori, Tagliapietra, Rizzoli, & Hudson, 2006) is the reduction of large-bodied mammalian hosts, namely wild ungulates (e.g. deer, elk). Ungulates often play a crucial role in tick life cycles, by providing the bloodmeal needed by adults of many species to survive and reproduce (Gray, 1998; Kiffner, Lödige, Alings, Vor, & Rühe, 2010)(Fig 1A). As ungulate populations are also relatively easy to manage (e.g. through hunting or culling), reducing ungulate abundance is often suggested in order to reduce tick densities (Kugeler, Farley, Forrester, & Mead, 2015; Stafford, Denicola, & Kilpatrick, 2003; Telford, 2017). However, studies that have investigated this relationship have found mixed results (Perkins, Cattadori, Tagliapietra, Rizzoli, & Hudson, 2006). In some cases, removing or reducing ungulates effectively reduces tick populations (Rand, Lubelczyk, Holman, Lacombe, & Smith, 2004), while in others, it has been found to have neutral (Deblinger, Wilson, Rimmer, & Spielman, 1993; Ostfeld, Price, Hornbostel, Benjamin, & Keesing, 2006; Stafford et al., 2003), or even positive effects on tick densities (Keesing, Allan, Young, & Ostfeld, 2013; Titcomb et al., 2017). Additionally, ungulate impacts on tick density appear to be climate-dependent (Titcomb et al., 2017), leading to divergent outcomes in different systems and increasing the challenge of predicting effects when climatic conditions are shifting alongside changing host assemblages, as is increasingly the case given global climate change. These disparate results confound our ability to implement effective management.

Testing the specific ecological mechanisms through which ungulate management impacts ticks under varying climatic conditions is thus a critical step to improving management for TBD. Work to date has largely focused on the direct impacts of ungulates on tick abundance through their role as a food source for ticks (Figure 1A). More recently, the indirect effects ungulates may have on food sources for nymphal and larval tick stages has received some attention, as it is increasingly recognized that ungulate reductions can drive compensatory (or more than compensatory) increases in small mammal hosts (Keesing et al., 2013; Perkins et al., 2006) (Figure 1B). Yet while it is well established that ungulates can transform habitats and ecological communities through consumption and trampling of vegetation (Coverdale et al., 2016), the indirect effects of ungulate herbivores on ticks through habitat modification has been largely untested. Notably, from the perspective of ticks, several of the pervasive effects of ungulate removal, including increasing plant cover, increasing shading, and reducing bare ground (Augustine & McNaughton, 1998; Jia et al., 2018), could strongly impact microhabitats critical to tick survivorship. Furthermore, these impacts are often context-dependent, with greater effects on vegetation structure under hotter and drier conditions (Elisabeth S. Bakker, Ritchie, Olff, Milchunas, & Knops, 2006; Burkepile et al., 2017; Maron, Baer, & Angert, 2014; Young et al., 2013), providing a mechanistic explanation for the context-dependent impact of herbivores on tick density that has been observed.

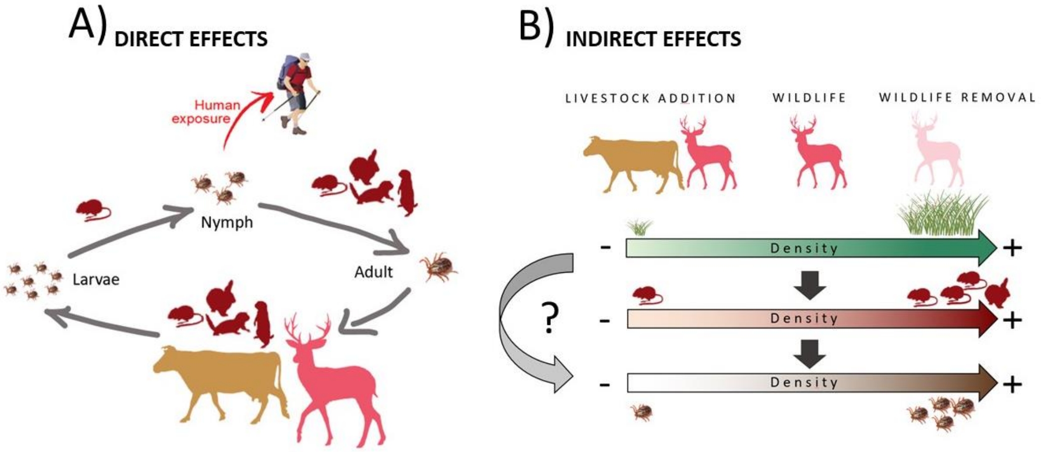


Figure 1. **Ungulates impact tick survival through multiple pathways.**

A) Directly, ungulates often serve as final hosts for adult ticks, potentially facilitating egg laying and reproduction; however, many ticks can use smaller host species, such that the absence of ungulates does not guarantee life cycle disruption. B) Indirectly, wild ungulate removal typically increases density of vegetation (green arrow) and thus small mammals hosts (brown arrow). The increase in vegetation may increase tick survivorship by reducing thermal stress for ticks off-host (grey arrow).

Notably, studies comparing the relative importance of host community and climate on ticks have found that in most systems, climatic conditions—not host availability— are the strongest drivers of tick populations and occurrence patterns, suggesting that indirect effects of ungulate removal in modifying microclimate may be more important for tick abundance than the direct effects of their loss as a food source (Hahn, Jarnevich, Monaghan, & Eisen, 2016; Nick H. Ogden & Lindsay, 2016; Nick H. Ogden et al., 2013). Consistent with this, at a local scale, tick abundances track favorable environmental conditions in heterogeneous landscapes (Kilpatrick et al., 2017; Parmesan & Yohe, 2003), resulting in patchy distributions wherein ticks inhabit advantageous microclimates within a larger habitat area. Specifically, habitat features that provide shading and reduce desiccation stress (e.g. understory cover, litter) best determine suitability of a given site for ticks (MacDonald, 2018). If ungulate removal primarily mediates tick survivorship via vegetation changes, we expect effects to be strongest: 1) in arid, low productivity sites where desiccation risk is high and plants are most impacted by herbivore grazing, and 2) for tick species that are especially sensitive to desiccation and/or near the arid extent of species' thermal range limits. The lack of research on the effects of ungulate herbivores on tick refugia and tick survivorship is surprising, particularly given how important climate is for tick survival, especially for juvenile life stages (Pollock, Gawne, & Taylor, 2015) which are the most sensitive to desiccation (Sonenshine, 2018). Notably, larval survivorship is itself much more tightly linked to human exposure risk than is the reproductive success of adult ticks (or the resulting abundance of larvae) (Guerra et al., 2002; Ostfeld & Brunner, 2015). Indeed, no correlation has been found between the initial abundance of larval ticks in one year and the subsequent abundance of nymphal ticks (the infectious stage of most human TBD), suggesting that larval *survival* to the nymphal stage is the critical parameter affecting TBD risk (N. H. Ogden et al., 2004; Nick H. Ogden & Lindsay, 2016; Ostfeld, Canham, Oggenfuss, Winchcombe, & Keesing, 2006). Thus, landscape management strategies that reduce larval survival to reduce nymphal cohort abundance (or reduce the duration of nymphal host-seeking) will likely have strong impacts on human–vector contact rates and tick-borne disease risk (Levi, Keesing, Oggenfuss, & Ostfeld, 2015; Salkeld, Porter, Loh, & Nieto, 2019). Specifically, for ungulate management, this suggests focusing on interventions that reduce larval survivorship—even if it increases adult tick reproductive success—particularly in contexts where larval survivorship responses to ungulate removal are high.

In this study, we used a large-scale herbivore exclosure experiment spanning three sites along a steep topoclimate gradient in southern California to examine whether manipulation of large herbivores can indirectly impact larval tick survivorship. We examined two regionally common tick species thought to have different thermal tolerances: *Ixodes pacificus* and *Dermacentor variabilis* (*I. pacificus* is believed to be more vulnerable to desiccation than *D. variabilis*) (Lane, Kleinjan, & Schoeler, 1995; Padgett & Lane, 2001). California is a suitable study system, as Lyme disease transmission risk is higher in parts of California than anywhere else in western North America (MacDonald et al., 2020). Moreover, the state is undergoing changes in climate regime and wildlife populations, and the majority of California's remaining grasslands are grazed by livestock, making the state a highly relevant location to examine effects of environmental change on tick dynamics. We predicted that the presence of wild and domestic large herbivores would drive changes in vegetation density and thus microclimate conditions, influencing juvenile tick survivorship rates. We hypothesized that complete removal of large herbivores would result in increases in understory vegetation density and associated shading by plants, creating habitat conditions leading to higher tick survivorship during the larvae life stage. Conversely, we hypothesized that large herbivores (both wild and domestic) would reduce vegetation and shading, reducing temperature and humidity levels at the soil surface, thereby reducing survivorship. We expected that both interventions would have stronger effects under the most arid climatic conditions, as shading by vegetation should be most critical for survival where thermal stress is greatest. We further predicted that effects should be stronger for the tick species more prone to desiccation stress (*Ixodes pacificus*). Cumulatively, this experiment provides critical insight into the interactive effects of large herbivores and climate on tick survivorship across multiple species.

3.3 METHODS

3.3.1 Study Site

Our research was conducted within the Tejon Ranch Exclosure Experiment (TREE), established in 2016 at Tejon Ranch in Kern County, CA (34°58´N, 118°35´W). The area is privately owned and managed by the Tejon Ranch Company for cattle ranching, hunting, and agriculture, as well as species conservation in partnership with Tejon Ranch Conservancy. The climate is Mediterranean, with hot, dry summers and cooler, wetter winters. Study plots encompass oak savanna-woodland (580-1675 m), dominated by a mix of *Quercus douglasii*, *Q. lobata*, and *Q. kelloggii*. Ponderosa pine (*Pinus ponderosa*) is also present (<10% canopy cover) at mesic sites. Understory is characterized by mixed exotic and native grasses and forbs (Bartolome et al., 2014) with woody shrubs becoming more dominant at higher elevations (> approx. 1372 m). Fires are infrequent, limited by reduction of fuel loads through grazing and active suppression of wildfire by land managers. 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).

Dominant ungulates in the study area include populations of mule deer (*Odocoileus hemionus*), Rocky Mountain elk (*Cervus canadensis*), pronghorn (*Antilocapra americana*), and feral pig (*Sus scrofa*), as well as an estimated 10,000 head (cow/calf pairs) of cattle spread across 72,000 acres of the ranch. Stocking density across the study area was approximately 0.13 head/ha (personal communication) during the study period. Cattle are free-ranging across the property, but moved seasonally to low elevation pastures in the winter (therefore, sites above approx. 1000 m in elevation are not grazed during the winter).

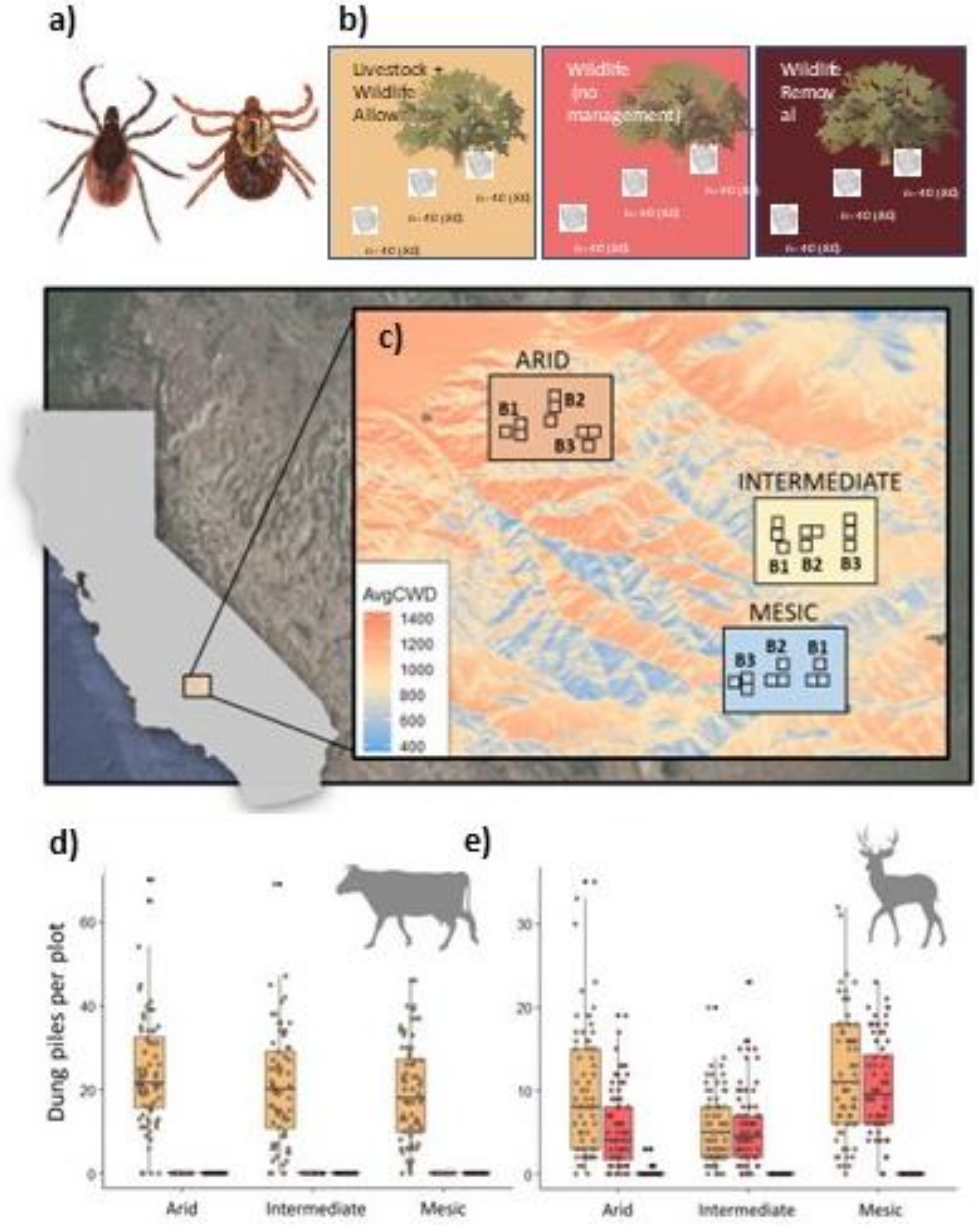


Figure 2. Overview of experimental design.

(A) In this experiment, we examined survivorship of two regionally common tick species, *Ixodes pacificus* (left) and *Dermacentor variabilis* (right). (B) Oak woodland plots were manipulated through fencing to either allow access to no large ungulates (simulating large-bodied wildlife declines or removals), only wild large ungulates (simulating no management), or both wild ungulates and domestic cattle. In each of these plots we installed three tick cages containing larval ticks of both species (standardizing for tree canopy cover). (C) Each treatment was replicated three times at each of three climate contexts (arid, intermediate, mesic), selected based on climate water deficit (CWD), projected at 250m resolution (McCullough et al., 2016), with a larger water deficit corresponding with hotter, drier conditions. (D, E) Dung counts of cattle (left-D) and wildlife (right-E) show that experimental plots function as intended.

3.3.2 Experimental Design

The TREE consists of three replicate blocks at three climate levels ("arid", "intermediate", "mesic"), each containing three 1-ha treatment plots (27 plots total). All sites are within 10 km of each other and vary in elevation from 580 m to 1705 m. At each climate level, the replicate blocks are 100–400 m apart. Treatments simulate the three most common forms of large herbivore change occurring globally. "Wildlife only" plots use a simple three wire fence that is completely accessible to native large herbivores (no significant differences in wild herbivores with and without this fence) but are non-permeable to cattle. "Total ungulate removal" plots use a five-wire fence design that is functionally inaccessible to all wildlife (95% reduction of individuals >40 kg compared to unfenced plots; Orr et al. *in press*). "Open" plots allow full access by both wildlife and cattle. Smaller herbivores (e.g. rodents, rabbits, birds, and grasshoppers) are not experimentally excluded from any plots.

3.3.3 Effects of Large Herbivores on Vegetation: Aerial Density

Vegetation has been monitored annually at the TREE in the spring, with prior results showing that increased ungulate activity tends to lead to increased bare ground, reduced litter accumulation, increased solar radiation, and reduced aboveground biomass, with these effects typically stronger in more arid contexts (Orr et al. *in press*). We expected that these changes in understory vegetation would be associated with changes in microclimate (temperature, humidity) relevant to tick survival.

We conducted vegetation monitoring using an established grid of 36 sampling quadrats, 1 x1 m in size (with 10 x 10 m spacing between grid points), at each of the 27 experimental plots. At each quadrat, we dropped five sample pins (150 cm in height), in the center and four corners of each 1-m^2 quadrat (total 180 pins per plot). For each pin drop, we recorded the number of times vegetation touched the pin (vegetation, e.g. grass, that paralleled the pin was given 1 "hit"; shrubs with multiple branches that crossed the pin were given independent "hits"). Sampling was done mid to late summer during the dry season (August and September 2018), concurrent with the experimental tick survivorship trial.

To investigate differences in aerial vegetation density across plots, we used generalized mixed effect models in R (package lme4; Bates, Mächler, Bolker, & Walker, 2015). Diagnostic tests of uniformity, dispersion, and outliers were performed with the DHARMa package (Hartig, 2019). Fixed effects included climate level, herbivore treatment, and their interaction, and we accounted for the site-level variation by including block as a nested random effect. Models were ranked by AICc, and R^2 values were generated with the package MuMIn (Bartón, 2013; Nakagawa, Johnson, & Schielzeth, 2017). P-values were estimated with the emmeans package (Length et al 2020).

3.3.4 Survivorship trials: unfed larvae

In July 2018, 6480 unfed larval *I. pacificus* and *D. variabilis* (3240 of each species) were provided by Centers for Disease Control and Prevention for distribution by BEI Resources (NIAID, NIH: *Dermacentor variabilis* larvae (Live), NR-44121; *Ixodes pacificus* larvae (Live), NR-44386). These larvae were randomly assigned to 3 cages in each of the 27 experimental plots at the TREE (Figure 3). Ticks were placed inside permeable silkscreen mesh bags sealed with tape following methods described by (Padgett & Lane, 2001). The mesh bags were hung inside 15 × 15 × 15 cm metal cages constructed from wire hardware cloth. The cages were intended to prevent predation on ticks from insectivorous arthropods, rodents and birds while still allowing the larvae to move vertically to avoid desiccation. All cages were buried with the tops of the tick bags flush with the soil surface, and leaf litter was restored to its pre-disturbed state. Each cage had 40 ticks of each species (120 ticks per species per plot; 3240 ticks per species total). In each plot, cages were distributed a minimum of 15 m apart and 10 m from the plot edge, and located to capture variation in tree canopy cover (0% cover, 30-50% cover, and >80% cover). Every two weeks, all cages were monitored for tick mortalities from deployment on July 28 through to censor (the date we terminated the experiment) on October 21. Ticks were considered dead if they appeared desiccated and did not respond to exhalation through the packet. The timing of the experiment corresponded with the presumed period of larval questing activity (e.g. August-October)(MacDonald & Briggs, 2016; MacDonald, O'Neill, Yoshimizu, Padgett, & Larsen, 2019).

We tested for effects of herbivore management strategy (livestock addition, wildlife only, total ungulate removal), site-level climate (arid, intermediate, mesic), and their interactions on larval tick survival using random effects Cox proportional-hazards regression models (Venables and Ripley 2010) to estimate the effects of site characteristics (aridity, herbivore management strategy) on hazard of loss, (which is related to tick longevity), using the "coxph" and "survfit" functions from the "survival" R package (Therneau and Lumley 2009), and tested for violations of the proportional hazards assumption using scaled Schoenfeld residuals, as calculated by the "cox.zph" function (Therneau and Lumley 2009). We built a global model with the predictor variables of herbivore treatment, climate category, tick species, and their pairwise interactions, and block and cage ID as random effects. Survival analyses were done using the "survfit" and "coxph" functions (Therneau and Lumley 2009. All analyses were conducted in R (R Core Development Team 2020). These methods of survival analysis are appropriate for assessing the impacts of multiple variables on survival time, allow the inclusion of right-censored data (where not all individuals were monitored through to the time of loss) and do not require that the data fit a particular survival distribution (Fox 2001). The general form of a Cox proportional-hazards model is a linear model for the log-hazard (Formula 1), where $h_i(t)$ represents the hazard of loss at time t (time since experiment onset) for each treatment plot (i):

$$\log h_i(t) = \alpha + \beta_1 x_{i1} + \beta_2 x_{i2} + \cdots + \beta_k x_{ik}. \qquad (1)$$

The constant *a* is the baseline hazard and the *x*'s are covariates that modify the baseline hazard. Because Cox proportional-hazards models are semiparametric, we used partial likelihoods in place of full likelihoods for our calculations of AIC values (Cox and Oakes,1984; Sargent, 1998). To determine which of the explanatory variables were important predictors of larvae longevity, we used Akaike's Information Criterion (AIC) (Burnham and Anderson 2002) and the MuMIn package (Barton 2020).

3.3.5 Effects of Large Herbivores on Microclimate

At each cage, we measured temperature and relative humidity weekly within 1 hour of solar noon (11:30 -13:30) throughout the experiment, using a handheld meter (DigiSense, Cole Parmer Scientific). The meter was held at the soil surface, beneath any existing vegetation or litter cover. We took five readings per cage: one directly atop the cage, and then one in each of the four cardinal directions within 0.5 m of the cage, and averaged these five readings to produce a measurement for each cage at each visit.

To determine whether there were differences in temperature and humidity across treatments, we used linear mixed models in R (package lme4). Temperature and relative humidity were the dependent variables respectively; climate level, treatment, and their interaction were fixed effects, with block as a nested random effect. We repeated model selection procedures described above.

3.3.6 Do herbivores impact tick survival through impacts on microclimate?

To investigate whether differences in ground level temperature and humidity were associated with changes in larval survival, we repeated the general procedure above for a second set of models which incorporated plot-level (the mean of the three cages per plot per visit) humidity and temperature measurements as time-varying coefficients, with block as a nested random effect (dropping climate category and herbivore treatment from this model due to collinearity among factors). We ran separate models for *Ixodes pacificus* and *Dermacentor variabilis*.

3.4 RESULTS

3.4.1 Vegetation responses

Ungulate herbivore treatments had a consistent impact on aerial vegetation density across the three climate categories, with highest vegetation densities within total ungulate removal plots, and modestly lower vegetation density with the addition of livestock (Figure 4A). The best fit model included treatment and the interaction among treatment and aridity level, with vegetation dramatically reduced in unfenced plots relative to partially fenced plots ($p<0.01$ for all within-level pairwise comparisons; Figure 4B). These results are consistent with patterns reported elsewhere for this system (Orr et al., *in press*).

3.4.2 Microclimate Conditions

Both livestock addition and complete ungulate removal altered temperature and relative humidity at the soil surface (microclimate). These effects were modulated by aridity level

(Fig 5), with effects generally strongest under high aridity. Changes in vegetation density appeared to impact midday temperature more than humidity (Figure 4; Figure 5).

Ungulate impacts on midday soil surface temperature were generally as predicted, with significant differences among all three herbivore treatments under arid conditions (p <0.0001 for all pairwise comparisons). At intermediate sites, both partial and total exclosures were cooler than plots open to livestock (open-total, p= 0.0364; open-partial, p=0.0121), while at mesic sites, there was only a notable difference among open and total exclosures (p=0.002). Temperatures were consistently lower inside total exclosure plots than in unfenced plots.

In contrast, ungulates had somewhat different impacts on relative humidity (Fig 5B). Overall, humidity was lower in unfenced plots than exclosures at the two climatic extremes, but not under intermediate climate conditions. At the most arid site, similar to temperature, there were significant differences among all three treatment types, however humidity levels were actually highest in plots only accessible to wildlife (Fig 5B). Under the most mesic conditions, there were significant differences between plots accessible to livestock and both partial and total exclosure treatments (p<0.0001 for both pairwise comparisons), but not between total ungulate removal treatments and plots accessible only to wildlife.

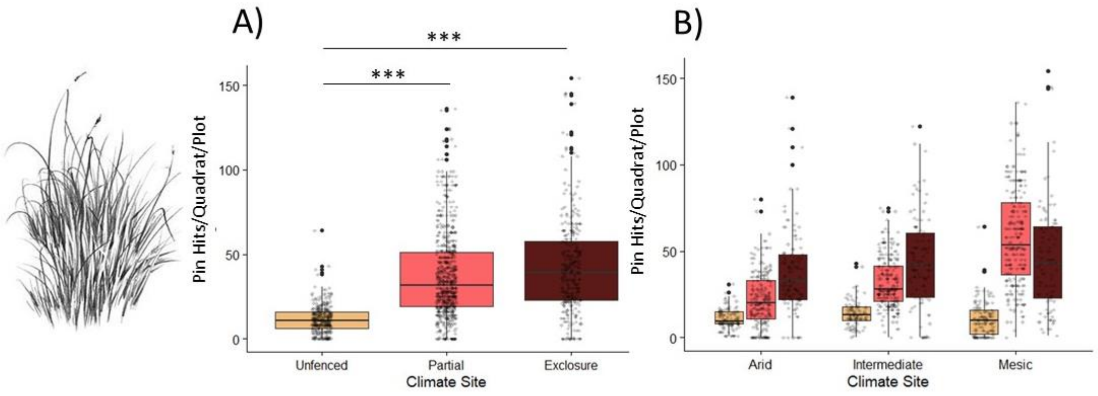


Figure 4. Herbivore removal had a significant effect on aerial vegetation density.

A) Overall, livestock addition significantly impacted aerial vegetation density relative to the two other treatments ($p < 0.0001$ for comparisons of livestock addition to wildlife only, and livestock addition to total removal). B) These impacts were significant even when site-level aridity varied. Livestock addition strongly decreased aerial density, while total ungulate removal modestly (but significantly) increased vegetation density at arid and intermediate climate levels, but decreased density at mesic, relative to plots accessible to wildlife (representing no active management). When climate level was not accounted for, there was no overall difference in vegetation density between wildlife only and total removal treatments. Asterisk denote levels of significance (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

3.4.3 Tick survivorship

Survivorship differed significantly between I. *pacificus and D. variabilis* ($p < 0.0001$, Supplement; Figure 6). This difference was driven by decreases in *I. pacificus* survival under higher aridity and in unfenced plots at arid and intermediate (Figure 7). For both species, larval survivorship rates were greatest at mesic and lowest at arid (Table 1). Overall, survivorship was greater inside exclosure plots and lowest in plots open to all ungulates at arid and intermediate, while conversely at mesic, there was no difference between unfenced and total exclosure plots.

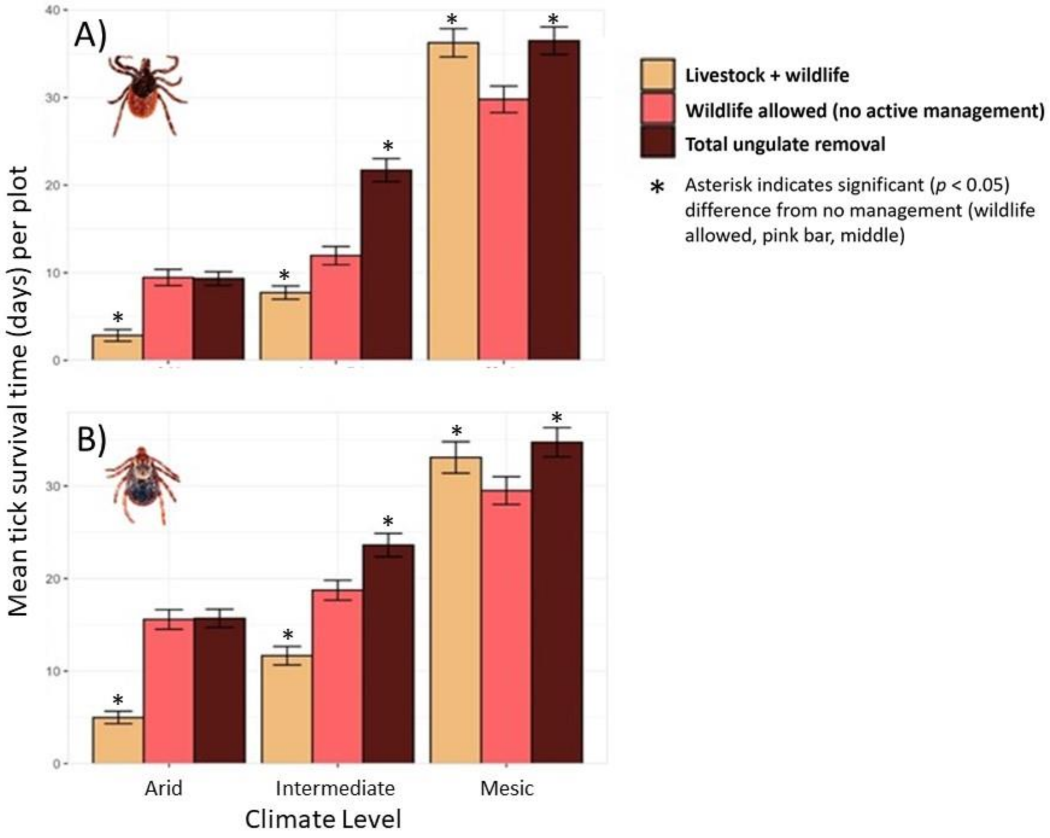
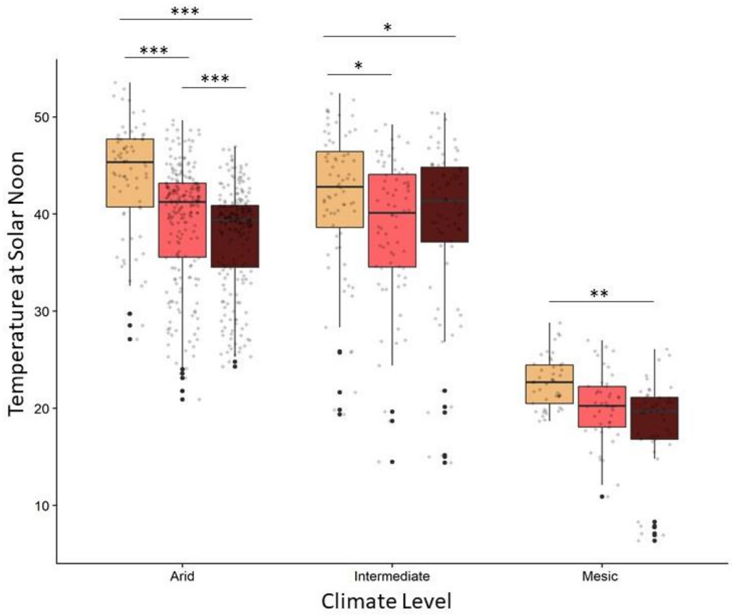


Figure 6. **Mean number of days that *Ixodes pacificus* (A-top) and *Dermacentor variabilis* (B-bottom) larvae survived within *in situ* experimental cages.**

Mortality patterns were similar for both species, though *I. pacificus* had lower survivorship under arid conditions than *D. variabilis*, as well as lower survivorship when ungulates were present at the intermediate level. At arid and intermediate climate levels, herbivore presence had a negative effect on survivorship. At the arid climate level, this effect was driven by cattle presence; at intermediate, wildlife had a negative effect and cattle presence increased this effect.

To better assess whether herbivores impact tick survivorship through their impacts on microclimate, we ran a second set of cox mixed effects models with temperature and relative humidity as predictors and block as a random effect. In this model set, temperature was the most important predictor of survivorship, while humidity was not a significant factor (Table 1). However, there was a significant interaction among relative humidity and temperature, suggesting humidity mediates the effect of temperature on survival of both tick species. As expected, greater temperatures generally corresponded with reduced survivorship.



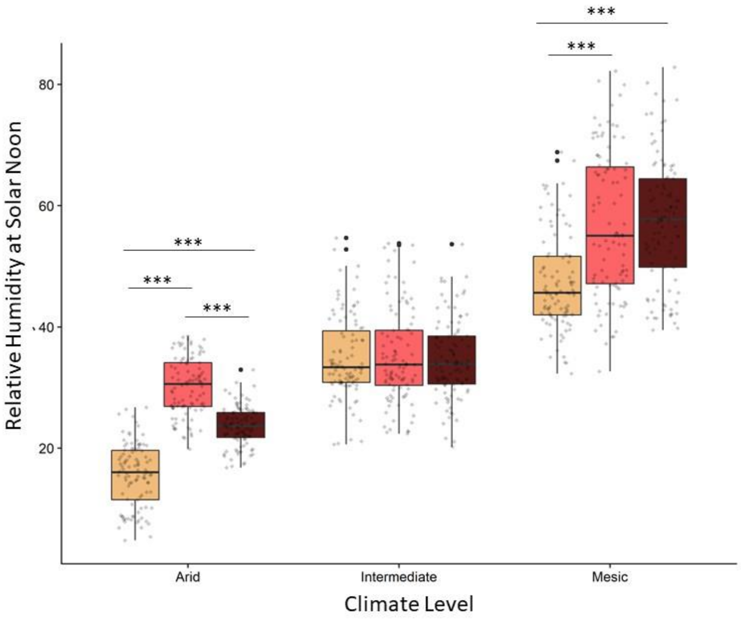


Figure 7: Herbivore treatments impact soil surface microclimatic conditions

Ungulate herbivores impacted temperature (top) and humidity (bottom) measured at midday at the soil surface. Ungulate impacts on these microclimate conditions relevant to larval tick survival were substantially mediated by topoclimatic conditions.

Species	**Factor**	**coefficient**	**SE**	**Z**	**P-value**
I. pacificus	**Exclosure**	**0.2611**	**0.0314**	**8.2700**	**<.0001**
	Climate Level	**-1.0042**	**0.0285**	**-29.944**	**<.0001**
	Exclosure:Level	**-0.0832**	**0.9786**	**-6.32**	**<.0001**
	Temperature	**0.03339**	**1.03395**	**2.533**	**0.0113**
	Humidity	0.00688	1.00691	0.795	0.4266
	Humidity: Temperature	**-0.00063**	**0.00029**	**-2.192**	**0.0284**
D. variabilis	**Exclosure**	**0.34709**	**0.044813**	**7.75**	**<.0001**
	Climate Level	**-1.5705**	**0.05892**	**-26.66**	**<.0001**
	Exclosure:Level	**-0.51541**	**0.10976**	**-4.70**	**<.0001**
	Temperature	**0.0294**	**1.0298**	**3.988**	**<.0001**
	Humidity	-0.00399	0.00581	-0.685	0.4930
	Humidity:Temperature	**-0.00061**	**0.00015**	**-0.685**	**<.0001**

Table 1. Best fitting Cox Proportional Hazard Models for tick survivorship for unfed larva, including coefficient estimate (b), standard error (SE), Wald's Z score (Z value) and P-value. Significant factors are in bold. Models were fitted separately for each species.

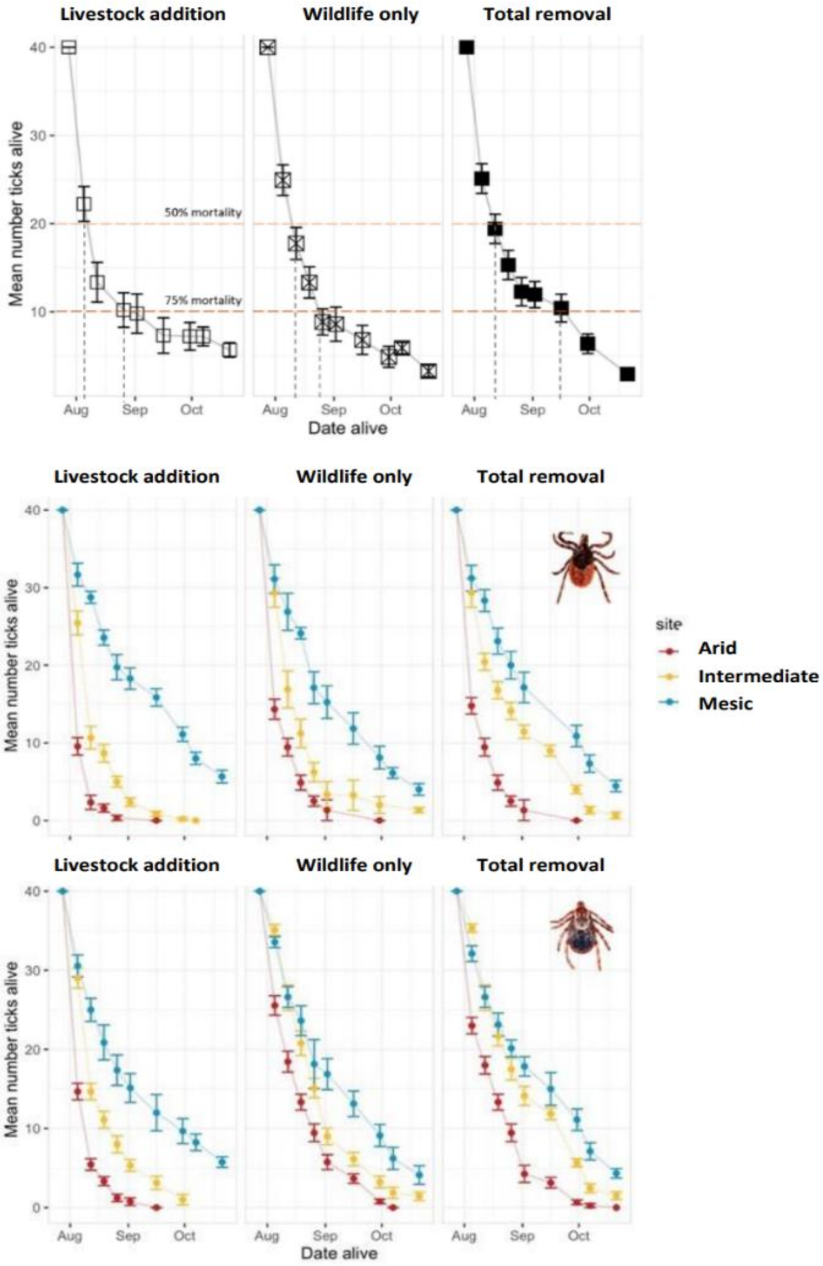


Figure 7. **Tick survival curves.**

(A-Top) Overall, ticks reached 50% mortality earliest in plots accessed by livestock and wildlife, and 75% mortality latest in total exclosure plots. This suggests that changing ungulate density via either wildlife removal or livestock addition can indeed indirectly impact survivorship rates. (B-Bottom) Survivorship rates varied clearly across climate levels, with lowest survivorship under arid conditions, and greatest survivorship under most mesic conditions. The effect of herbivore treatment varied by climate level as well, with herbivores having stronger negative impacts on survivorship under more arid conditions. This was apparent for both Ixodes (middle) and Dermacentor (bottom) ticks.

3.5 DISCUSSION

With the recent emergence and acceleration of TBDs diseases across the globe (Fang et al., 2015; Kugeler et al., 2015)—there has been increasing interest and need to develop effective landscape management strategies for TBD prevention. Much of this attention has focused on manipulation of ungulate hosts, through hunting or culling, or acaricide treatment in the specific case of livestock. Yet, despite clear connections among vegetation, microclimate, and tick survival, using ungulate grazing to reduce tick survivorship has been, to our knowledge, largely ignored. Our findings thus have strong implications for disease management. Indeed, host management is a popular control strategy for a number of additional diseases relevant to humans and animals, including mosquito-borne diseases (the top vector of disease to humans). Because of the widespread use of and interest in host management, understanding its efficacy and potential for unintended consequences is of tremendous social and environmental importance.

We use an experimental approach to investigate the efficacy of two ungulate management strategies—wildlife removal and livestock addition—in controlling survivorship of two regionally common tick species, *Ixodes pacificus* and *Dermacentor variabilis*, across a topoclimate gradient in an ecologically diverse region of California. We find ungulate management strategies can have strong effects on survivorship of both tick species, but these effects vary substantially depending on climatic context. As we predicted, drier, warmer conditions appear to reduce larval survival and amplify the suppressive effects of ungulate herbivores. Under more mesic conditions, ungulates had a less clear effect on tick survivorship.

3.5.1. Ungulates govern habitat features relevant to tick survivorship

Our results showed that ungulates strongly impact vegetation density and microclimate relevant to tick survivorship. Understory density increased with decreases in ungulates; specifically, vegetation density is 20-50%lower when livestock are allowed (compared to wildlife only plots). Our observed vegetation responses indicate traditional management practices of complete removal of ungulates may have unintended consequences: for example, increases in vegetation in the absence of ungulate herbivores have been observed in other systems to increase rodent density (E. S. Bakker, Olff, & Gleichman, 2009; Keesing, 1998; Parsons, Maron, & Martin, 2013; Smit et al., 2001). If the longer juvenile tick survival times we observed in this study are indicative of patterns elsewhere, these two indirect effects of large herbivore removal may actually accelerate TBD transmission.

In addition, increased vegetation typically provides more shading, buffering temperatures near the soil surface where ticks spend 90-95% of their life (Ostfeld & Brunner, 2015). Humidity was impacted by herbivore treatment at the arid and mesic extents of our study, but not under our intermediate climate condition. The mechanism for this is unclear, given that herbivores had a consistent effect on vegetation density across climatic contexts, but may be related to the specific composition of the plant community at the intermediate site and differences in leaf area, moisture content, or other plant traits relevant to moisture exchange; or other factors (e.g. soils, additional trophic interactions) that we did not account for. Previous work has robustly established the importance of humidity (both atmospheric and vegetation-derived) for tick survivorship; it is likely that the lack of importance in our results is therefore due to factors we did not fully measure, such as diel temporal trends in humidity (e.g. dew points) at these sites (as our temperature and humidity measurements provide only a ‘snapshot’ of conditions). Overall, these results suggest that ungulates can impact microclimate relevant to ticks through their impacts on understory vegetation and that these effects vary in magnitude across climatic contexts.

3.5.2. Ungulates affect tick survivorship, and livestock in particular, reduces survivorship in arid contexts

Our results show that both wildlife addition and livestock removal alter tick survivorship, but that effects are highly dependent on climate context and that livestock addition has particularly strong impacts on larval survivorship. We highlight the particularly strong effects of livestock addition in arid environments. Reducing larval tick survivorship, especially during dry season questing periods, should reduce the length of time available to larvae to find a host, and thus, have the potential to disrupt disease transmission cycles by creating a bottleneck at the larva to nymph transition stage in the life cycle (MacDonald & Briggs, 2016). Decreases in fine-scale temperature and humidity will require questing ticks to return more frequently to the leaf litter to rehydrate, making host-seeking more energy intensive (Nick H. Ogden & Lindsay, 2016; Padgett & Lane, 2001), perhaps leading to truncated periods of host-seeking; however, these impacts are only relevant for juvenile tick survival in locations of high to moderate aridity. Our results suggest that in regions of California where current conditions are comparatively hot and dry, such as in southern California or interior regions of central and northern California (e.g., the Northern California Interior Coast Ranges), vegetation density and microclimate may be key limiting factors for juvenile survival and potentially duration of host-seeking activity. In arid areas, incorporating livestock grazing—particularly near the edges of range limits for ticks and pathogens of concern—may have a large impact as a TBD control measure.

In contrast, in regions where current climate is cooler and wetter such as higher elevation grasslands and woodlands in the central coast or northern California, microclimate conditions may be much less limiting for juvenile ticks than in arid regions (MacDonald et al., 2019). Under mesic conditions, both wildlife removal and livestock presence appeared to slightly increase tick survivorship—though the mechanism here is unclear— indicating that under such conditions, conservation of intact wildlife communities may be the best mechanism to reduce TBD prevention. These results align with the results of previous studies highlighting regional variability and potential nonlinearity in the response of disease vectors to environmental change.

3.5.3. Contrasting effects of wildlife and livestock: identity vs density

Our findings illustrate that the addition of livestock does not ‘substitute’ for wildlife. It is difficult to parse whether this is due to identity differences and different diet preferences and foraging behaviors, or due primarily to the differences in density between wildlife and cattle or both. Cattle are present at much higher densities foraging in a single area more consistently than wildlife, and thus the addition of livestock has consistently stronger effects than the removal of wildlife. For all response variables measured, the difference between livestock addition plots and total ungulate removal plots was consistent, while sometimes there was no difference between wildlife-only presence vs total removal. This suggests that, under some conditions, the effects of cattle and wildlife are additive. Working alongside rangeland managers to experimentally manipulate stocking densities and seasonal timing of grazing would further elucidate the role of livestock in suppressing tick survivorship and by extension, TBDs. Our results also suggest wildlife and livestock have unexpected impacts under more mesic conditions, and future work is needed to parse why livestock have a positive effect relative to wildlife on tick survival in these environments.

3.5.4. Strength of response varies by tick species

Notably, our data suggest that the efficacy of grazing management as a tool for altering tick survivorship varies could vary by tick species. In our experiment, *I. pacificus* larva were overall more sensitive to environmental stress than *D. variabilis,* experiencing increased mortality rates especially under drier conditions. This is consistent with known physiological constraints *of I. pacificus,* the western blacklegged tick (Padgett & Lane, 2001), which should make it particularly susceptible to microhabitat changes. Increasing temperatures and aridity in already hot and dry regions will lead to declines in habitat suitability (MacDonald, McComb, O'Neill, Padgett, & Larsen, 2020). Consistent with this, in our results *D. variabilis* followed a similar trajectory to *I. pacificus* in response to the grazing treatments, but exhibited somewhat higher survivorship under arid conditions. This species-specific variation is important for targeted management of specific diseases: *Ixodes*-spread pathogens (such as Lyme) may be more effectively managed by grazing than *Dermacentor*-vectored pathogens (such as Anaplasmosis or Rocky Mountain Spotted Fever) under arid conditions.

3.5.5. Management as a TBD control strategy

Management strategies including livestock grazing, or removal of understory vegetation by other means, are likely to be more effective where ticks are already climate-limited. Warming climates are expected to shorten the window during which ticks can survive off-host (MacDonald et al 2018). Increasing grazing could, in turn, further reduce pathogen transmission through vertebrate hosts and ultimately infection prevalence in tick populations. Hotter and drier conditions may also influence host-seeking behavior, for example by shifting larval and nymphal tick host-seeking from aboveground vegetation to below the leaf litter surface (I. M. Arsnoe, Hickling, Ginsberg, McElreath, & Tsao, 2015; Lane, Fedorova, Kleinjan, & Maxwell, 2013; MacDonald & Briggs, 2016), thereby substantially reducing human tick encounter risk (I. Arsnoe, Tsao, & Hickling, 2019). Human encounter risk is a significant factor in TBD transmission, and thus, any efforts that minimize risk of human encounter may be beneficial in disease mitigation. By reducing vegetation cover and litter accumulation, livestock grazing could further shorten questing and reduce host encounter rates. It is possible that reductions in understory biomass may also reduce abundance of small mammal hosts (Bakker et al 2009; Young et al 2015), leading to shifts in host feeding for some tick life stages—for example from small mammals to lizards—which could dramatically alter pathogen transmission dynamics across western North America (Swei et al., 2020; Swei, Ostfeld, Lane, & Briggs, 2011). However further research is needed to assess this pathway as that is well beyond the scope of this study.

Our finding that grazing-driven reductions in vegetation impact ticks and thus potentially TBD transmission builds on recent studies investigating the impacts of similar vegetation reductions by other means, including wildfire. In both the case of fire and grazing, there is evidence that removal of understory vegetation has a substantial impact on TBD through multiple pathways. For instance, fire-induced understory loss can suppress the density of competent hosts (MacDonald et al., 2018), but effects may be lagged leading to changes in disease risk through time. It is worth noting that annual understory removal over multiyear time scales is likely needed for tick life cycle disruption (due to their 3-year life cycle length), and seasonal timing of understory removal also matters for tick survivorship and questing activity; in our study system, grazing management meets these requirements, but this may vary in other locations.

3.5.6. Caveats

Our results show strong evidence that ungulate grazing can, in some cases, reduce tick survivorship, providing support for a relatively unappreciated mechanisms by which ungulates may reduce, rather than increase, disease risk. However, due to the complex lifecycle of ticks and the multiple pathways by which ungulates may impact ticks, we emphasize these results alone cannot predict the net effects of ungulates (wild or domestic) on tick abundance, much less disease risk in these landscapes. Future research on landscape level tick abundance of multiple life stages and pathogen prevalence within these life stages will be needed to understand net effects of ungulate abundance on TBD. Further, because this work was conducted in a relatively narrow window of time (summer-fall) during the driest part of the year, results may not be predictive of dynamics occurring elsewhere if larvae are active in the winter or other seasons. However, at a minimum, these results, combined with mixed effects of ungulate removal from other studies, strongly argue that ungulate removal should not be assumed to lead to a reduction in ticks. Additionally, this study cannot argue for the net benefits of grazing in a given landscape – as clearly benefits and costs of grazing are diverse and context dependent and out of scope of this study. In combination with other studies, this advances our understanding of the complexity of TBD transmission and the impact of large herbivore manipulation as an environmental control strategy.

3.6.7. Implications and Synthesis

Understanding, predicting, and managing for infectious tickborne diseases is imperative for protecting human health, and curbing the global rise in TBD. The need to mitigate TBD is likely to increase as human land-use pressure escalates and human encounters with wildlife and the wildland interface become increasingly common. Fully elucidating tickborne disease transmission cycles remains difficult due to their complexity and the likelihood of nonlinear responses across vectors, vector life stages, pathogens, and hosts. However, this work illustrates a simple pathway through which land managers might be able to reduce risk, via reduction of understory though grazing (or other means) in high-risk areas and especially in drier sites and thus reducing tick survivorship. In complex, multi-use landscapes that are home to complex herbivore-tick-plant assemblages, we found that ungulates herbivores—both wild and domestic— suppress larval tick survival. While more research is needed to understand whether this reduced survivorship translates to changes in landscape level disease risk, these results suggest that there is a strong mechanistic pathway for such a relationship. Specifically, these results suggest that, at least in some contexts, culling of ungulates may have adverse outcomes on tick survivorship and perhaps disease risk. Instead, wildlife conservation, in some contexts augmented by domestic grazing, may have beneficial effects on tick-borne disease suppression.

Authors' Contributions:

DO, AS, ED, and HY designed the study. DO, ED, SC, AB, and CM collected and collated the data. ZZ and DO analyzed and interpreted the data. DO, AB, and ZZ created figures. All authors participated in drafting, revising, and approving the final draft of the manuscript.

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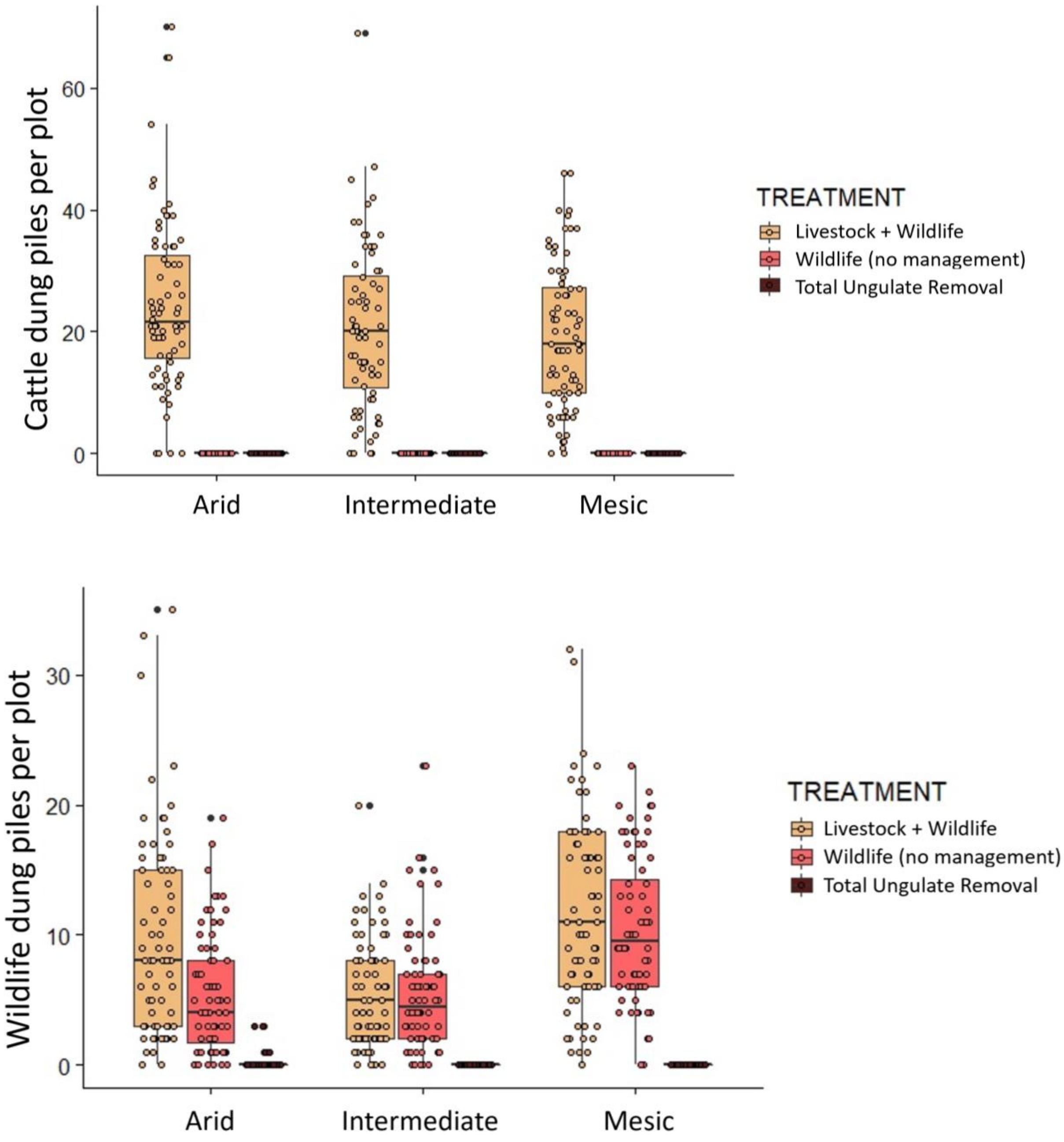
CHAPTER THREE: APPENDIX

Appendix A

Appendix, Figure 1. Large Herbivore Activity and Efficacy of Herbivore Exclosure Experiment. Vegetation density changed visibly in response to ungulate manipulation in the study area from 2016 to 2018. Photographs from summer 2018 of (A) plots accessible to cattle and wildlife, (B) plots accessible to wildlife (but not cattle), and (C) plots that are fully fenced to remove all ungulates. Note the relatively large increase in understory biomass when cattle are absent, in comparison to much smaller increases in plant abundance in plots excluding all ungulates. When livestock and wildlife were present, there were large patches of bare ground, little litter accumulation, and reduced vegetation cover, density, and biomass. In contrast, plots with wildlife but not livestock had much greater vegetation cover and litter accumulation. (C) Complete removal of ungulates modestly increased vegetation density and further reduced bare ground.



Appendix, Figure 2. Dung piles were counted seasonally in each plot from early 2017 to spring 2019. Dung counts demonstrate overall patterns of ungulate activity consistent with the intention of the experiment: cattle are active in plots open to wildlife and cattle, but not inside exclosures; wildlife are active in both open and partial exclosures, but mostly not inside total removal plots. Wildlife appear to prefer plots accessible to livestock in Arid blocks, but there is no difference in wildlife activity among open and partial exclosures at Intermediate or Mesic blocks. Wildlife appear to be slightly more active at Arid and Mesic than at Intermediate.

Appendix B

Appendix, Table 2: Final model terms, error structures, and marginal and conditional coefficients of determination (R^2) for linear and generalized linear mixed effects models predicting 1) vegetation aerial density 2) midday temperature and 3) midday humidity. Marginal and conditional coefficients of determination give the variance explained solely by the fixed effects, and by all model terms (i.e., random and fixed effects) respectively. Treatment refers to herbivore exclosure type; level refers to climate level (arid, intermediate, mesic).

Response Variable	**Final Model Structure**	**Error Structure**	**Marginal R^2**	**Conditional R^2**
Plant aerial density (pin hits)	Aerial density ~ Treatment + Level + Treatment*Level + (1| Level/Block)	Poisson	0.7965575	0.8710153
Soil Surface Est. Max Temp (solar noon)	Log(Temp) ~ Level + Level*Treatment + (1| Level/Block)	Gaussian (Log-transformed)	0.7540874	0.8476397
Soil Surface RH (solar noon)	RH~ Level + Level*Treatment + (1| Level/Block)	Gaussian	0.5525624	0.7758613

Response Variable	**coefficient**	**SE (coefficient)**	**z**	**z Pr(>|z|)**
Species (IXPA vs DEVA)	0.27232	0.02570	10.597	< 2e-16 ***

Appendix, Table 3: Terms for the model investigating the effect of species on survivorship.

Appendix C.

Photographs illustrating habitat differences among “arid”, “intermediate”, and “mesic” sites.

Arid:

Intermediate:

Mesic:

Climate (averaged across all plots)	Elevation (m)	Total Annual Precipitation (mm)	Mean daily minimum temp	Mean daily maximum temp	mean daily average temperature	mean daily maximum vapor pressure deficit	mean daily minimum vapor pressure deficit
Arid	848.78	352.61	9.25	22.34	15.80	4.94	22.87
Intermediate	1581.78	418.89	6.70	18.62	12.66	4.13	18.07
Mesic	1668.11	430.20	6.56	18.47	12.52	4.12	17.95

Appendix, Table 4. PRISM climate data interpolated and averaged over 1997-2017

PRISM climate data for our three experimental sites including: total annual precipitation (ppt), average daily maximum temperature (tmin), mean daily minimum temperature (tmax), mean daily average temperature (tmean; tmax+tmin/2), mean daily maximum vapor pressure deficit (vpdmin), and mean daily minimum vapor pressure deficit (vpdmax). The data are interpolated from an 800m resolution for the years of 1981-2010. PRISM performed the interpolation for tmin, tmax, tmean and ppt using a digital elevation model as the predictor grid. Interpolation of vpdmin and vpdmax was collected using the daily mean dew point, tmin, and tmax as the predictor grids.

We performed ANOVAs using the car R package (Fox et al., 2020), using Tukey’s HSD postdoc tests to determine significance between climate sites.

Mean daily minimum temperature was nearly 3C higher at the warmest site than the coolest site. Total annual precipitation varied significantly by climate site (Intermediate-Arid, $p < 0.001$; Mesic-Arid, $p < 0.001$; Mesic-Intermediate, $p < 0.001$), with Mesic having the highest values followed by Intermediate, and then Arid.

CHAPTER 4: WILDLIFE AND CATTLE STRUCTURE AVAILABILITY OF FLORAL RESOURCES, BUT EFFECTS ARE MODULATED BY TOPOCLIMATIC CONDITIONS AND HERBIVORE TYPE

4.1 ABSTRACT

1. Large ungulate herbivores can both directly and indirectly impact plant community composition and structure in savannas and rangelands, with strong knock-on effects. One such potential effect is the production of floral resources, which in turn has significant impacts both on animal pollinators, as well as feedbacks through pollination services and plant reproduction.

2. We examined how wild ungulates and cattle affect the availability and diversity of floral communities (flowering plant density, diversity, composition) and a critical floral resource, nectar sugar content, at a set of large herbivore exclosure plots replicated along a topoclimatic gradient in a semiarid savanna in southcentral California. This study has three types of 1-ha experimental plots: wildlife-only, cattle and wildlife (all large herbivores), and no large herbivores.

3. Here, we show that excluding large mammalian herbivores *decreases* floral density and diversity under arid conditions, has a *neutral* effect under intermediate conditions, and has varied effects under more mesic conditions depending on herbivore treatment, with highest densities when only wildlife are present. Similarly, herbivore removal drives community composition shifts through changes in both turnover and nestedness, but these shifts are modulated by climatic context. Finally, changes in floral composition, diversity, and density result in net changes in plot-level nectar (sugar) production, with significant

increases when only wildlife are present at arid, stepwise reduction in nectar sugar availability with partial and total herbivore exclusion at intermediate, and *decreased* nectar sugar when livestock were present relative to partial and total exclosure treatments at mesic.

4. Our results suggest that both livestock addition as well as complete removal of all large herbivores may be deleterious for floral resource production under some contexts while being beneficial in others. This study documents a novel set of ecological interactions that demonstrate how both conservation and livelihood goals can be met in a working landscape with abundant wildlife and livestock so long as abiotic context is accounted for. Global changes in wildlife populations, rangeland extent, and climatic conditions are likely to interactively alter floral resource production, with potential consequences for pollinators and related ecosystem functions/processes.

4.2 INTRODUCTION

Wild ungulate herbivore populations are declining in many grassland and savanna systems worldwide, driven in part by wildland conversion to rangeland and replacement by livestock. Livestock grazing is now the most widespread landuse on Earth (Asner et al., 2008), with livestock now comprising over 90% of the planet's non-human mammalian biomass (Bar-On et al., 2018). Across the world's rangelands, livestock continue to replace wildlife, potentially with negative impacts on plant and animal communities and ecosystem structure and function (du Toit & Cumming, 1999; Hempson et al., 2017). There is now extensive research indicating large herbivores frequently act as keystone species, exerting substantial impacts on plant communities through grazing, trampling, and nutrient redistribution (Jia et al 2018, Koerner et al 2018, Orr et al, in press). These shifts then lead to an important question: how do these changes cascade across grasslands/savannas to impact species interactions, food chains and ecosystem functions?

One such “herbivore-initiated interaction cascade” (Pringle et al., 2007) may be via alteration of floral resource availability for pollinators, with knock-on effects on pollinator communities, plant-pollinator interactions and provisioning of pollination services/plant reproduction. Floral resources—i.e. pollen and nectar—have been strongly linked to pollinator community composition, visitation rates and plant-pollinator network structure, and provisioning of pollination services (Kearns et al. 1998, Steffan-Dewenter et al. 2005, Schweiger et al. 2010, Neuschulz et al. 2016). Pollination in turn is crucial to the maintenance of diverse plant communities (Balvanera et al., Kremen 2005), such that a reduction in floral resource availability could create negative feedbacks impacting biodiversity conservation of both plants and pollinators: an estimated 60–80% of wild plants and 35% of global crop production depends on animal pollination (Kearns et al. 1998, Ashman et al. 2004, Klein et al. 2007). Many current strategies to combat pollinator declines (Vogel et al 2017) focus primarily on enhancing floral resources (Baude et al 2016; Kaiser-Bunbury et al., 2017), and pollination has been identified as one of the most threatened processes of plant reproduction (Neuschulz et al 2016). Given these concerns, understanding whether wild and domestic herbivores impact floral resource production is important for multiple conservation and management efforts.

Large herbivores may impact floral resources through multiple pathways. Directly, herbivores can impact floral resources via consumption of leaf or reproductive tissues (Flemming et al., 2006), reduce plant density through trampling and consumption (Goheen et al., 2013) and prompt plants to reallocate energy to growth in lieu of reproduction. Evidence from pastoral landscapes largely suggests that livestock suppress plant-pollinator interactions (Vanbergen et al., 2016; Oleques et al., 2019). On the other hand, large herbivores may also *indirectly* shape floral resources via alteration of plant competitive dynamics (Borer et al., 2014; Koerner et al., 2018). Grazing herbivores (e.g. cattle) that predominantly remove biomass of the dominant plant species may be more likely to increase or have mixed effects on facilitation of flowering plant species through mediation of the competitive environment, for instance by increasing the attractiveness of floral displays, quality of floral rewards, and the availability of foraging niches (Neuschulz et al., 2016; Kremen et al., 2007; Potts et al., 2003). In contrast, herbivores that are browsers or mixed-feeders (e.g. deer, elk) may more selectively consume palatable rare or high-nectar content species, which could negatively impact floral resources and plant-pollinator interaction networks (Louthan et al., 2019; Guy et al., 2021). Though, at larger scales they might also increase floral diversity by maintaining more heterogeneous vegetation (cite). Such impacts by large herbivores on community-scale resource production may strongly govern plant-pollinator dynamics and the successful provisioning of pollination services. Thus, a better understanding of these relationships is needed in order to preserve this critical function for future ecosystems in this era of rapid global change.

Furthermore, recent global syntheses have illustrated that impacts of herbivore losses and additions are context-dependent, mediated by plant community characteristics (e.g. species dominance, life form, functional group), and abiotic site conditions (e.g. precipitation, temperature, topography, soils). Thus, there is strong potential for synergies among shifting herbivore assemblages and other drivers of global change, including climate change. For example, herbivores typically exerting stronger control on plant dynamics in more arid environments (Bakker et al., 2006; Young et al., 2013; Daskin & Pringle, 2016), and in systems dominated by one or two highly palatable species (Koerner et al., 2018).

While previous studies have independently investigated the effects of wild and domestic herbivores on individual flowering plant species (Wilkerson et al., 2013), there remains a need to scale up from these species-specific results to fully understand how these interactions manifest at the community scale. Furthermore, though the effects of wildlife on plant-pollinator networks under varying precipitation levels has been recently explored (Guy et al., 2021), to date the impacts of large herbivores and livestock on floral resource production (nectar sugar) have not been jointly examined within a single controlled experiment, nor have these relationships been simultaneously explored across climatic gradients to evaluate the relative context-dependence of these impacts.

In this study, we experimentally tested how wild and domestic large ungulate herbivores affect floral community diversity, composition, and floral resource availability in a semi-arid oak savanna ecosystem in California (Tejon Ranch Conservancy, Kern County). Critically, this is the location of an existing herbivore exclosure experiment, "TREE", which manipulates access to cattle and wildlife in replicated 1-ha plots across a strong topoclimatic gradient. Here, we tested the following hypotheses: (i) Large herbivores have significant impacts on floral communities and floral resources; (ii) These impacts vary depending on herbivore type (wild or domestic), due to known differences in feeding strategy (mostly grazing cattle vs mixed grazing-browsing wildlife) as well as stocking density (higher densities of cattle than wildlife will drive stronger effects); (iii) There are interactions between abiotic site conditions and the effect of large herbivore declines and livestock additions on floral communities and floral resource production.

4.3 METHODS

4.3.1 Field site

We experimentally tested how native and domestic large herbivores affect floral communities and floral resource availability in a semi-arid California oak savanna ecosystem (Tejon Ranch Conservancy, Kern Co., CA, USA). This region is a floristic and pollinator biodiversity hotspot (Myers 2000) of high conservation priority: Tejon hosts at least 911 native plants—14 percent of the native flora of California occurring on just 0.25 percent of the state's acreage—and over 1000 species of bees, with iconic wildflower displays each spring. Tejon is an active cattle ranch and also hosts healthy populations of mule deer (*Odocoileus hemionus*), Rocky Mountain elk (*Cervus canadensis*), and pronghorn (*Antilocapra americana*), as well as introduced feral pigs (*Sus scrofa*). Aridity (climate water deficit, temperature, precipitation, heat load index) varies across the conservancy, with changes driven by variation in topography (slope, aspect, elevation). This region is already experiencing warming and drying climates, with anticipated warming of up to 3C over the next century (McCullough et al., 2015). This site therefore offers an excellent opportunity to better understand how human activities (livestock introduction, wildlife declines, climate change) systematically investigate the cascading effects of large wild herbivore declines and livestock introductions in the Anthropocene, with results that are highly relevant to both regional and global conservation efforts.

4.3.2. Experimental design

We quantified the effects of large herbivores on floral resources, and the role of aridity in modulating these interactions, using an existing ungulate exclosure experiment, TREE (Orr et al, in press). This series of fenced 1-ha herbivore exclosures and unfenced control plots was established in 2016 and is replicated in blocks from low elevation blue oak savanna (more arid) to higher elevation south-facing (less arid) and north-facing (least arid) valley-black oak savanna-woodland. Elevation ranges from 550m (arid) to 1730m (intermediate, mesic). This experiment contains three treatment types: 1) total exclusion of all large herbivores (deer, elk, pronghorn, feral pig, cattle) using barbed wire fencing, 2) partial exclusion of cattle, but not wildlife, using lower fencing, and 3) unfenced plots, open to all wildlife and cattle. Three blocks (each containing one replicate of each treatment) spaced 100 to 450 m apart are located at each of three sites along the topoclimatic gradient. The experiment thus comprises a total of 27 1-ha plots.

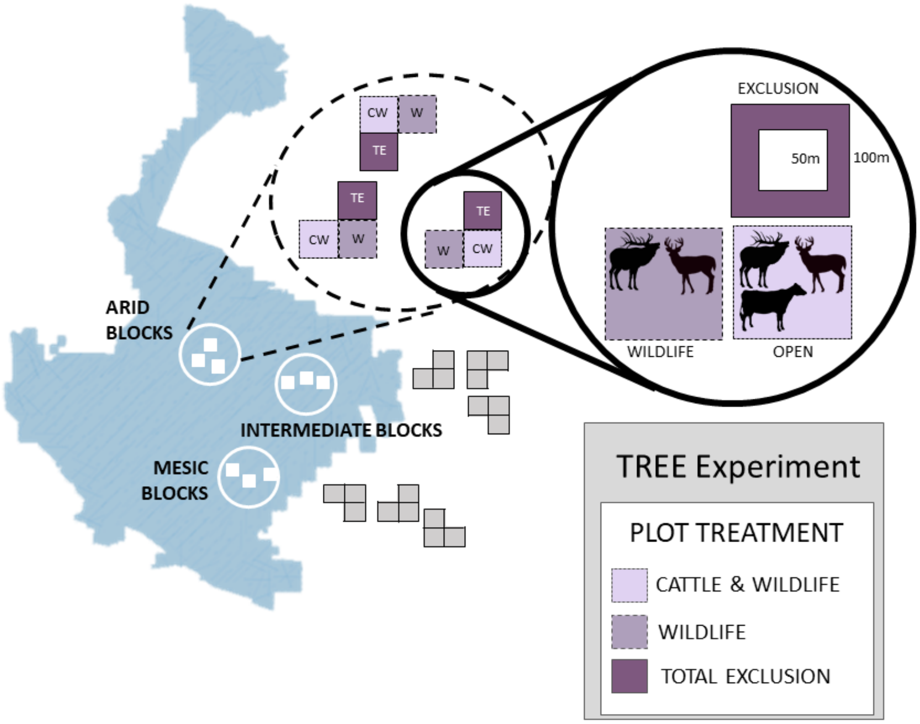


Figure 1. **Map of experimental plots.**

TREE plots (100 x 100m; 1ha) are located at three sites (Arid, Intermediate, Mesic) and each site contains three blocks of experimental treatments. Each block of the experiment contains three 1ha plots that differ in treatment: total-exclusion (TOTAL EXCLUSION; where all adult wild and domestic ungulates are excluded), partial-exclusion (WILDLIFE; where wild ungulates are allowed but cattle are excluded) and open (OPEN; where all ungulate herbivores have access) plots. Arid sites are characterized by higher climate water deficit (CWD) than intermediate sites, which have a greater water deficit than mesic sites. Changes in CWD are driven by differences in topography: arid is on a relatively flat, low elevation plateau, while intermediate and mesic are at a higher elevation, but intermediate is on a south-facing slope and mesic on a north-facing slope in the same drainage basin. To ensure that our data reflected each treatment, we restricted our sampling of each 100 x 100 m (1 ha) plot to a 50 x 50m (0.25 ha) subplot located at the center of each plot, which is illustrated as the central, white square in the EXCLUSION plot of the expanded block (top right).

4.3.3 Data collection

Sampling floral communities: Three years into the experiment, we conducted six 50m x 2m belt transects within each 1 ha plot once a month from March-May (arid), or April-June (intermediate, mesic), timed to capture the peak of flowering for all spring-flowering species within plots (with general timing of surveys based on prior year observations). During these surveys, we counted the number of fully open, non-senescing flowers of each species. For analyses, we took the high count from these three surveys for each species to yield a “peak” floral availability (e.g. we did not consider temporal variation in resources).

Measuring nectar of each flowering species: We quantified nectar for the majority of flowering species within experimental plots (rare species present in < 5% of surveys were excluded). Nectar was collected from a minimum of ten single flowers from different individuals for each species between 0900-1600 hours; these had been bagged (using 1.4 x 1.7mm fabric mesh) for 24h to prevent depletion by nectar-feeding insects. When possible (Supplement T1), glass microcapillaries (1.5 mL) were used directly to collect the nectar, otherwise single flowers were washed with 2 mL of distilled water and agitated for one minute within a 20mL sterile vial, and the diluted nectar solution was collected (Morrant et al., 2009; Power et al 2017). The sugar concentration of nectar was measured by using a hand-held refractometer modified for small volumes (Eclipse, Bellingham and Stanley, Tunbridge Wells, UK), and subsequently corrected for dilution to determine μg sugar per flower (per 24 hr period) (Phillips et al 2017).

4.3.3 Statistical analyses

Effects of ungulate herbivores on floral diversity (alpha diversity)

To determine how the floral assemblage species richness and Shannon diversity differed between open, partial exclusion, and total exclusion plots, and to assess the potential topoclimatic-site dependence of these effects, we constructed linear mixed models (LMMs) with block as a random effect using the R package "lme4" (Bates et al 2015). For each metric, we constructed four candidate models that included experimental block (i.e., paired total exclusion, partial exclusion and open plots) nested within site (Arid, Intermediate, or Mesic) as a random effect and fixed effects of herbivore treatment type, site, and the interaction term (Supplement Table 2 & 3). We performed residual diagnostics (including checks for heteroskedasticity and dispersion) for each candidate model using the "DHARMa" package (Hartig 2020). To assess how herbivore treatment and climate site influenced the species richness and diversity, we compared candidate models with and without each predictor variable using one-sided likelihood-ratio tests with the anova function in R, with alpha values set to 0.05 for significance testing, as well as through AICc comparison of all candidate models ("MuMIn" package; Barton 2020).

Effects of cattle and wildlife on floral β-diversity and its components (nestedness, turnover)

We used permutational distance-based multivariate analysis of variance (PERMANOVA; Anderson, 2001), using the function "adonis" from the package "vegan" (Oksanen et al. 2016) in R, to examine whether plots with more dissimilar species communities were associated with herbivore treatment. The strengths of these relationships were analyzed based on the partial R^2, and the significance was estimated using 999 permutations. Due to high known turnover of species among the three topoclimatic sites, we conducted this analysis separately for each site to isolate the effect of herbivore treatment on composition change. In addition to overall dissimilarly, we partitioned β-diversity into its two components, nestedness (i.e. species loss between treatments) and replacement (species change between treatments), using the beta.multi.abund function from the "betapart" statistical package (Baselga et al 2021) in R (R Core Team 2020). We account for species abundances to provide more useful information on the mechanisms shaping diversity patterns within and among communities (Ulrich and Gotelli 2010, Baselga 2013). Nestness (β_{SNE}) in this situation represents a measure sensitive to species gains or losses, whereas turnover (β_{SIM}) represents a richness-independent measure of replacement differences in species composition (Baselga 2013). We used the Sorensen index for nestedness and turnover calculations. We ran PERMANOVA analysis using herbivore treatment as a factor, block as a random effect, and the three distance matrices as response variables.

Do cattle and wildlife alter floral resource availability?

Floral density and total μg nectar sugar per ha: We examined effect of treatment, site, and their interaction on total flowers and total μg sugar per plot using generalized linear mixed models (GLMMs) with the package "glmmTMB" (Brooks et al 2017), specifying a negative binomial distribution following examination of residual diagnostics (including checks for heteroskedasticity and dispersion) for each candidate model using the "DHARMa" package. To assess how herbivore treatment and climate site influenced the s, we followed the same model selection process described above.

4.4. RESULTS

4.4.1 Effects of ungulate herbivores on alpha diversity

Herbivores had a significant effect on species richness, but this was modulated by topoclimatic site and varied by herbivore treatment (Fig 2). At arid blocks, removal of wildlife decreased richness. The addition of cattle had no significant effect on richness in comparison to wildlife-only plots, but there was a significant difference among open and total exclusion plots (Fig 2). Conversely, at mesic removal of wildlife had no effect on richness relative to plots with wildlife, but the addition of cattle significantly decreased richness relative to both partial and total exclusion treatments. The best fit model included treatment, site, and their interaction and block as a random effect (Appendix).

Similarly, herbivores had a significant impact on Shannon diversity of floral communities under some contexts, but the overall pattern across treatments and climate sites was unlike the relationship observed for richness. Herbivores had no impact on Shannon diversity at arid, the addition of cattle slightly increased diversity relative to total exclusion plots at intermediate but neither total exclusion nor open plots were significantly different from partial exclusion plots with wildlife only; and at mesic, total exclusion decreased diversity relative to wildlife-only and open plots (Figure 3). However, despite the significant difference in treatment at mesic, the top fitting models included only site and the random block effect (Appendix), suggesting spatial factors were more important than herbivore interactions in structuring floral Shannon diversity. Across topoclimatic sites, Shannon diversity was lower at arid than at intermediate or mesic (Figure 3).

4.4.2. Effects of cattle and wildlife on floral β-diversity and its components

The relationship between removal of cattle and wildlife and plant species composition also varied between topoclimatic sites. PERMANOVA analysis found a significant relationship between Bray-Curtis dissimilarity and herbivore treatment at arid (adjusted $R^2 = 0.19$; $F_2 = 38.19$; $P < 0.001$), intermediate (adjusted $R^2 = 0.08$; Treatment, $F_2 = 13.62$, $P = 0.001$), and mesic ($R^2 = 0.14$; Treatment, $F_2 = 25.48$, $P < 0.001$).

At arid, herbivores impacted both nestedness ($R^2 = 0.11$; Treatment, $F_2 = 31.05$, $P < 0.05$) and turnover ($R^2 = 0.18$; Treatment, $F_2 = 36.24$, $P < 0.001$), with the greatest difference in species between plots open to wildlife and cattle and exclosure treatments (Figure 6, A-B). In turn, communities within total exclosures contain a subset of the species that occur within partial exclosures. In other words, the removal of wildlife correlated with increased nestedness, while the addition of cattle was associated with increased turnover. At intermediate, herbivores significantly impacted β-diversity through primarily changes in nestedness ($R^2 = 0.09$; Site, $F_2 = 13.80$, $P < 0.05$), rather than turnover, as can be visually seen in Figure 6, C-D. Here, total plots contain a subset of species found in partial plots, which in turn, contain a subset of species found in open plots. At mesic, dissimilarity among herbivore treatments was due largely to turnover ($R^2 = 0.10$; Treatment, $F_2 = 20.03$, $P < 0.01$), rather than nestedness ($R^2 = 0.04$; Treatment, $F_2 = 26.36$, $P = 0.52$). This shift is driven by cattle presence in open plots; there was no significant difference in composition between partial exclusion plots open to wildlife and total ungulate exclusion treatments (Fig 6, E-F).

4.4.3 Do cattle and wildlife alter floral density?

Herbivores had a significant impact on the total number of flowers per plot, but this varied strongly across climate sites (Figure 4). Under arid conditions, cattle addition increased total floral density while total removal of ungulate herbivores decreased floral density; but neither addition nor removal significantly differed from wildlife-only plots. While we observed the same general pattern at intermediate climatic blocks, the relationship there was not strong enough to be significant. At mesic blocks, the addition of cattle notably decreased total floral density relative to wildlife-only (partial) plots, and while total ungulate exclusion also appeared to lead to a decline in floral density, there was no significant difference between total exclusion and open or wildlife-only plots (Figure 4). The best fit model for total flowers had a negative binomial error structure and the fixed effects of treatment, climate site, and their interaction, and random effect of block (Appendix).

4.4.4 Do herbivores affect total μg nectar sugar per ha (total flowers per species x g sugar per flower per species) across topoclimates?

While similar, total g sugar from nectar differed in substantial ways from total floral density patterns. At arid, nectar sugar availability was greatest when wildlife-only were present (partial exclosures) and lowest when all herbivores were absent (Figure 5). At intermediate, there was a significant difference in nectar sugar among all three herbivore treatments, with greatest availability when both wildlife and cattle were present and similar to arid, lowest availability when all ungulates were excluded. At mesic, partial exclusion plots open only to wildlife had the highest nectar sugar availability, while plots open to livestock had the least (Figure 5). Notably, while total flower density was similar at arid and mesic sites, total nectar sugar availability was actually much higher at mesic than arid or intermediate. Similar to total flower density, the best fit model included a negative binomial error structure, and treatment, climate site, and their interaction as fixed effects, and block as a random effect (Appendix).

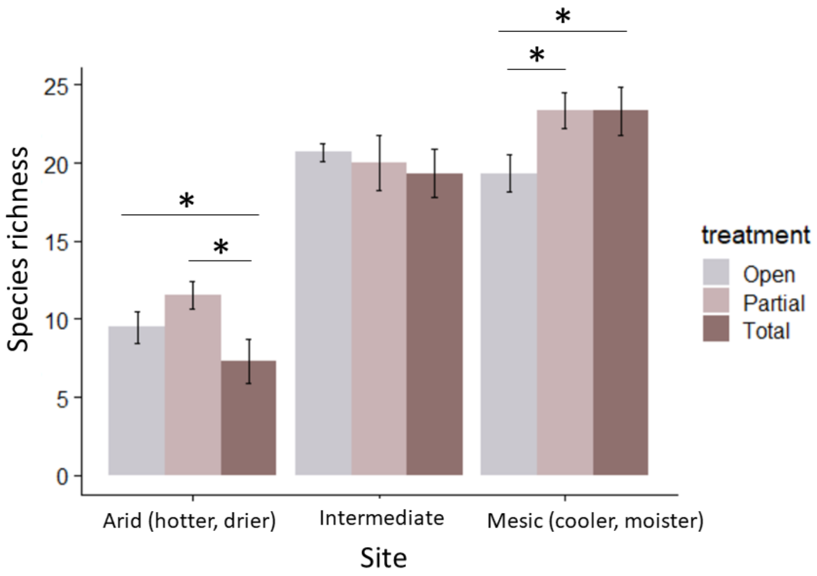


Figure 2. Herbivore removals affected floral richness.

Complete herbivore exclusion reduced species richness at arid blocks, while conversely, exclusion of cattle and all herbivores increased richness at mesic blocks.

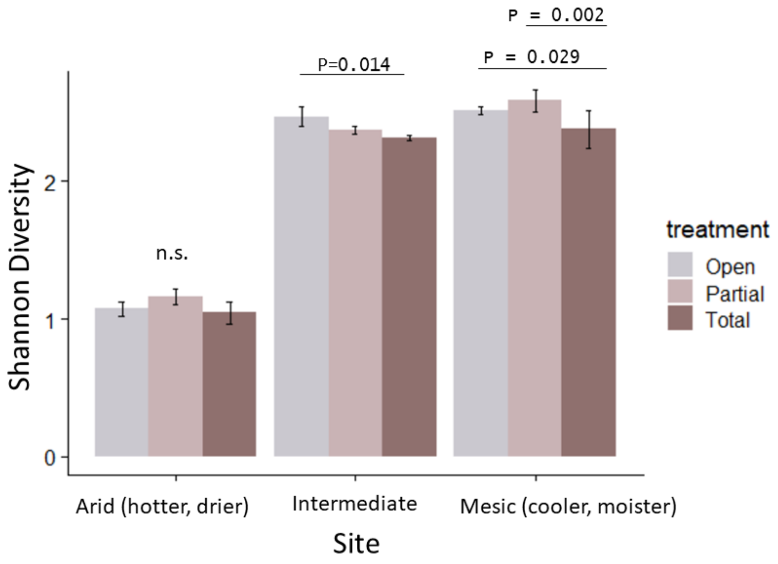


Figure 3. Herbivore treatments affected Shannon diversity.

Effects of herbivore removal were not significant at arid, but were significant at intermediate among exclosures and open plots, and at mesic among partial and total exclosures and total exclosures and open plots.

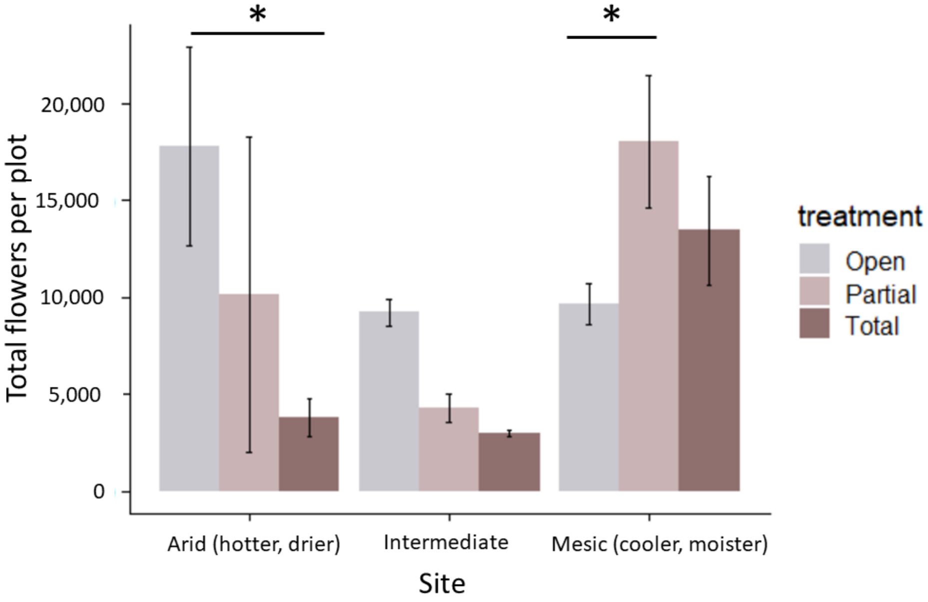


Figure 4. Total floral density per experimental plot.

Plots open to livestock and wildlife had highest floral densities at intermediate and arid, but conversely, lowest densities at mesic.

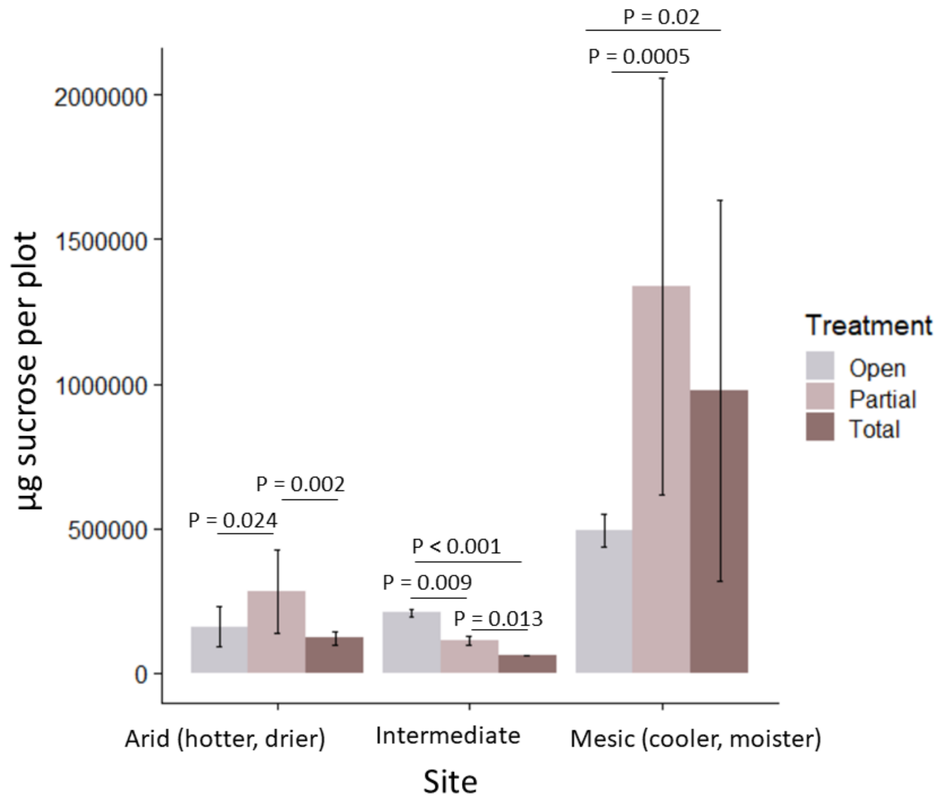


Figure 5: Floral nectar availability at the plot scale.

Floral resource availability was significantly impacted by herbivore treatment, with highest nectar content in plots open to wildlife (but not cattle) at arid and mesic, while at intermediate, plots opwn to livestock had highest nectar availability.

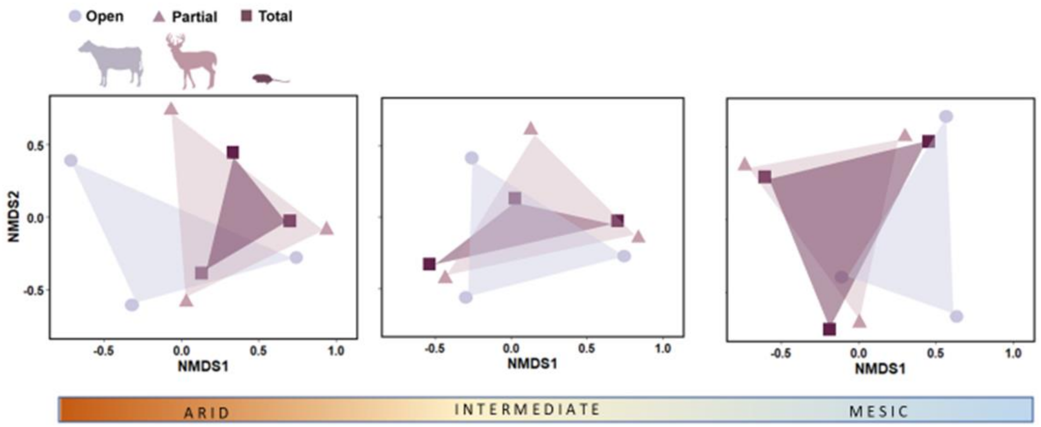


Figure 6. nMDS plots of floral communities across climate levels.

Community composition of floral communities shifted depending on herbivore treatment, but the changes differed across climatic levels, which great dissimilarity among open plots and exclosures at mesic.

4.5 DISCUSSION

Our results show that global declines in large wild ungulate herbivores and increases in domestic livestock like cattle have the potential to strongly impact floral resource availability, but the magnitude and direction of these impacts are strongly modulated by abiotic context. In support of our hypotheses, we found that the complete loss of ungulate herbivores can create effects that cascade to pollinators particularly under hotter, drier environmental site conditions. In turn, our results further show that the addition of novel domestic herbivores—in this, cattle—can create interaction cascades as strong or stronger than those driven by species losses, with cattle presence driving different impacts on floral resource diversity, composition and production than wildlife on their own.

4.5.1 Positive vs Negative Effects of Herbivores on Floral Communities and Nectar Production

Our results from counts of total flowers per plot at the two drier sites (arid, intermediate) support previous experimental work from savannas in Kenya finding that herbivores can impact floral assemblages (Louthan et al., 2019) and that relative to wildlife, cattle increase floral density (Wilkerson et al., 2013). Based on these and other findings (e.g. Guy et al 2021), we had expected that wildlife, as browsers, would consistently reduce floral density, diversity, and floral resources through direct consumption. Large herbivores can negatively impact floral resources via consumption of leaf or reproductive tissue, which can reduce appeal or value to pollinators by 1) reducing photosynthetic ability, thus decreasing the energy that can be invested in floral resources (Brys et al., 2011); 2) delaying flowering (Scheper et al., 2015) and 3) damaging reproductive structures, such as causing malformations in corolla or tube shape (Potts et al., 2010); although some studies have shown herbivory can have direct positive impacts as well, as consumption of senescing material can enhance plant longevity, biomass production, and reproductive investment (Louthan et al., 2013; Goheen et al 2018) increasing plant fitness and investment in floral resources. Surprisingly, none of the responses we measured were lowest in wildlife-only treatments, and wildlife presence corresponded with *highest* resource availability under the coolest, wettest conditions in the TREE. From these results, it appears that indirect pathways may be outweighing any negative impacts of direct consumption by wildlife. Wild herbivores can maintain vegetation heterogeneity via selective consumption of vegetation (Karzinel et al., 2015; Pringle et al., 2016), shade- and risk-sensitive space use (Ford et al., 2016) and nutrient redistribution (le Roux et al., 2020), all of which produce patchy mosaics of plant biomass and species composition. Thus, the negative effects of browsing wildlife observed elsewhere may be partially offset here due to the relatively large spatial scale (1-ha) of our experimental plots, wherein we are able to capture heterogeneity caused by grazing and trampling, which opens space for a greater diversity of less-dominant forbs.

Extending this to consider the effects of both wildlife and cattle, Koerner et al (2018) found that large herbivores tend to positively impact plant diversity when they consume dominant species in a community. Fahnestock and Knapp (1994) found that bison herbivory on grasses indirectly facilitates forb growth through increased light availability and reduced competition in tallgrass prairie. Other studies support the idea that grazing by large native or domestic ungulates increases biodiversity of forbs (e.g., Collins et al. 1998; Hickman et al. 2004; Manier and Hobbs 2007). In California grasslands and savannas, dominant species consist largely of exotic grasses (*Bromus* spp), which may exclude flowering species in the absence of herbivores. Indeed, in the TREE plots, complete herbivore exclusion has increased vegetation cover, aboveground biomass, litter, and shading (Orr et al, in press), all of which may help to explain the negative effects of total ungulate exclusion on floral resources.

4.5.2 Climate-dependence of Herbivore Impacts

As we expected, topoclimate strongly modulated both the magnitude and effect direction of livestock and wildlife. Interestingly, the differences in cattle and wildlife effects from arid to mesic are potentially explained by indirect climate effects, namely turnover in plant species composition across these sites related to water limitation (and other climate-driven factors). This results in dominance shifting from exotic grasses towards co-dominance with *Ericamera nauseosa* at intermediate and by *Ribes roezlii*, a flowering shrub, at mesic; such that plant-plant interactions differ with community turnover along the topoclimatic gradient.

Differences in palatability, reproductive strategy, and other traits of the dominant plant species in a community may therefore dictate whether wildlife and cattle have positive or negative impacts on overall floral communities and resource production. Future work that takes a trait-based approach could be used to generate a more predictive framework based on floral traits for determining responses to herbivory across systems. Ultimately, more studies are needed that complement our mechanistic experimental approach by evaluating large-herbivore effects on floral resources, plant-pollinator networks, and pollination services across many more sites and a gradient of ecosystems with varying ungulate biomass density, ungulate identity, abiotic conditions, and anthropogenically altered disturbance regimes.

In addition, climate has a number of direct effects that may further interact with the community-level patterns we found. Plants in environmentally stressful conditions may already be producing fewer flowers, have shorter flowering windows, or allocate fewer overall resources to reproduction (Phillips et al 2018); thus direct consumption likely most impactful in stressful environments where plants can't readily recover. While previous studies have independently investigated the effects of herbivores on individual plant species (for example, Wilkerson et al 2013), our study fills a gap by scaling up from these species-specific results to investigate how these interactions manifest at the community scale. However, the partitioning of energy and resources between growth and reproduction in immediate response to grazing pressure and abiotic stress manifests strongly at the scale of individual plants, so in addition to changes in species composition, changes in individual plant physiology and resource investment may have substantial impacts as well. For example, impacts at the flower scale are likely to affect pollinator foraging behavior due to changes in the reliability of nectar reward. Though we did not explicitly explore this in this study (e.g. we counted total flowers per species, but not total flowers per individual plant), such sources of nectar variation may be useful to consider particularly when thinking about interactions among herbivory and climate. Many studies that have demonstrated changes in nectar volume in response to water availability (Carroll et al., 2001; Gallagher & Campbell, 2017; Villarreal & Freeman, 1990), and that nectarless flowers can be produced in response to environmental stress (Petanidou & Smets, 1996; but see Takkis et al.,2015). This may have factored into the lower nectar sugar amounts measured at arid and intermediate relative to mesic, combined with the community-scale differences in species composition. Due to our blocking design we cannot formally separate the effect of topoclimate from the effect of experimental site, and so we do not attempt to tease apart whether climate itself drives variation in floral nectar and flowers. However, it is worth noting that relatively fine scale variation in abiotic conditions (topoclimatic variation at the scale of ~300m) can strongly mediate nectar production and it would be good to separate whether this is through interspecific variation, intraspecific variation, or both. Such knowledge would be valuable when thinking about landscape-scale conservation plans.

4.5.3 Implications and future directions

Given these findings, we can infer multiple impacts on both pollinators and pollination. There has been considerable concern over declines in insect pollinator communities and potential impacts on the pollination of crops and wildflowers (Biesmeijer, J.et al, 2006; Potts et al., 2010; Vanbergen et al., 2013) and decreasing floral resources has been suggested as a key contributing factor (Goulson et al., 2015; Carvell et al., 2006). Given the global extent of wild ungulate population changes and intensification of landuse for livestock, our results show that there is substantial room for herbivore management for pollinator conservation through provisioning of floral resources. Responses to herbivory are often plant species-specific—which indeed, we observed here—such that the impacts of herbivores on plant communities appear to depend on species composition (Grime et al., 2000). For example, a greater diversity of plant strategies may provide greater community resilience to both herbivores and abiotic stress (Phillips et al., 2018), including in the provision of floral resources. Changes to the diversity and quantity of floral nectar that we observed may affect individual pollinators (Vaudo, Tooker, Grozinger, & Patch, 2015) and the diversity of the pollinator community (Ghazoul, 2006). Changes in the overall availability of floral resources, which affects the amount of food that is available to pollinators, will certainly have consequences for pollinators at the population level (Baude et al., 2016; Carvell et al., 2006,2017; Roulston & Goodell, 2011), and likely, on pollinator diversity and plant-pollinator networks (Ponisio et al., 2016; Guy et al., 2021). These changes can drive further impacts on pollination and plant reproduction (e.g. seed set, viability of seeds), which we would expect to be strongest for plant species that rely most heavily on animal pollination.

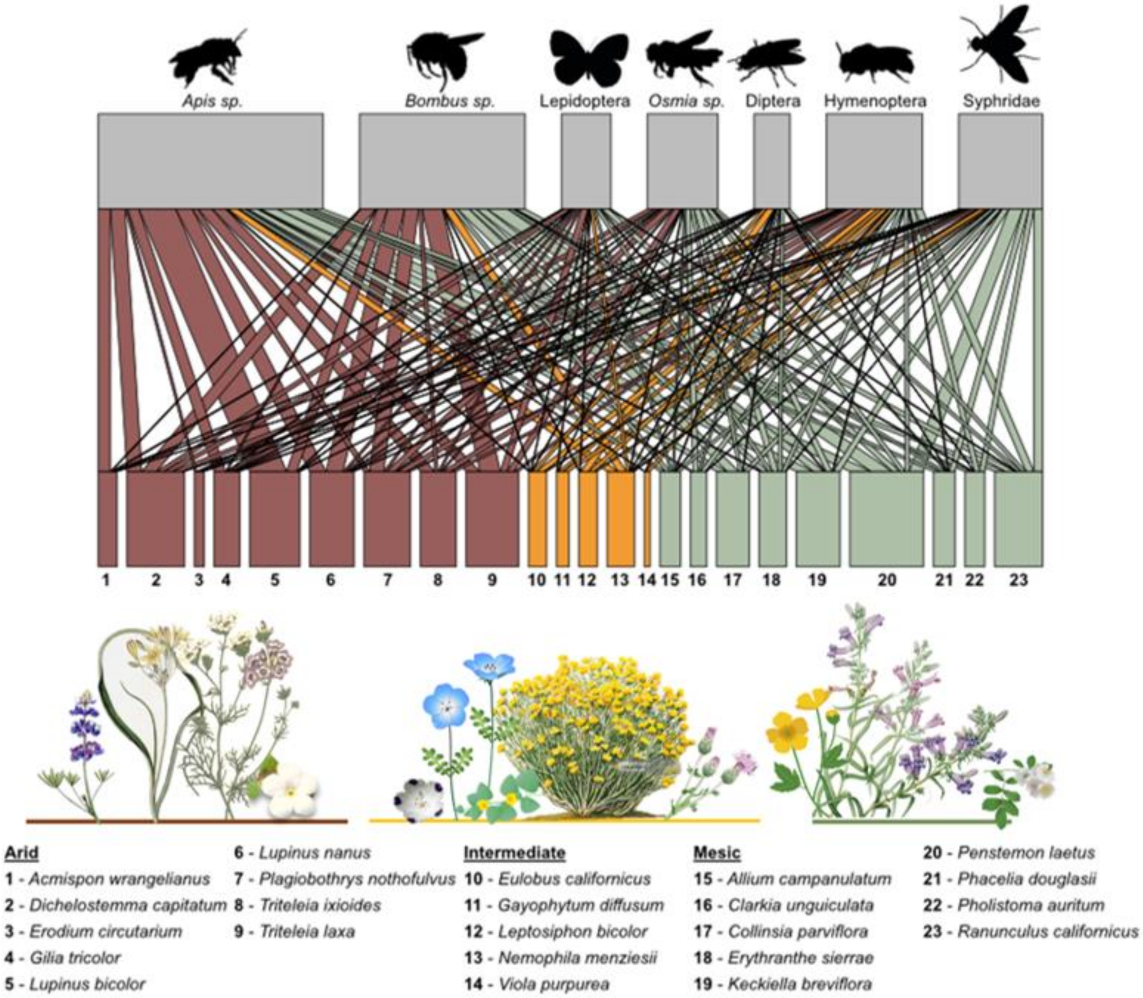
To our knowledge, this is the first study to concurrently examine the effects of cattle and wild ungulates across varying climatic conditions on floral resource production within a single an experimental setting. The advantages of our study are that it involves intact experimental plant and wildlife communities based in situ in a temperate region undergoing real shifts in herbivore assemblages and climatic conditions. However, this does come with disadvantages: for example, it is difficult to disentangle effects of herbivore selectivity, identity, and density to determine which of these is driving the differences among plots open to cattle and wildlife and partial exclusion treatments (open to wildlife). Despite this, our results capture realistic, large-scale patterns of shifting landuse and biodiversity, such that these results are still applicable for management and conservation (even without identifying which aspect of the herbivore assemblage shift is most impactful). Use of new methods for characterizing animal diets (e.g. Karzinel et al., 2015; Miller-ter-Kuile et al, in review) may be helpful for understanding the exact mechanisms through which elk, deer, cattle, and other herbivores shape floral communities, and could be particularly beneficial for managing livestock to promote floral and pollinator diversity. Study of cattle impacts across different stocking densities would help elucidate possible critical grazing thresholds for different plant species and plant communities, and would help to isolate the effects of cattle grazing from other ungulates. An additional limitation is that we focused on quantifying "peak" floral resource production. However, any impacts of herbivory and climate on flowering timing and duration, and stability of floral resources through time, certainly would be tremendously important, and should be the focus of future work. Finally, a salient next step in this system is explicitly linking these changes to pollinator communities, pollination—a key ecosystem process—and the effects of climate, wild, and domestic herbivores on the stability and resilience of plant-pollinator mutualist networks in grasslands and savannas of western North America and beyond.

4.5.4 Conclusions

This study highlights the strong and interacting effects of large herbivore shifts along climatic gradients on plant communities, and extends previous work by linking these impacts on plant communities to the production of floral resources, a useful proxy for plant-pollinator interaction network structure and pollination processes. Around the world, wild and domestic herbivores have myriad impacts on vegetation diversity (Augustine & McNaughton 1998; Anderson, Ritchie& McNaughton 2007); faunal communities, including insects (Pringle et al. 2007); plant–animal interactions (Palmer et al. 2008); and ecosystem function and stability (Forbes et al 2019; Goheen & Palmer 2010). As large herbivore assemblages continue to shift globally, it is crucial to understand the magnitude of the effects these assemblage changes will have on entire ecosystems. Building a better picture of how both wild and domestic large herbivores indirectly and directly influence a multitude of ecosystem functions, including nectar production and pollination, will be key to developing feasible conservation and management strategies for maintaining ecosystem function and stability amidst ongoing global change.

Supporting Information

Figure S1. Bipartite network of plant-pollinator interactions observed for herbaceous plant species. Red = Arid, Yellow = Intermediate, Green = Mesic. Plant species with the greatest visitation rates included at mesic: *Penstemon laetus* (mountain blue penstamon) and *Keckiella breviflora (*bush beardtongue), which were negatively associated with cattle presence, and *Ranunculus californicus* (California buttercup), which was positively correlated with livestock and negatively correlated with partial and total exclosures. At arid, *Dichelstemma capitatum* (blue dick), *Lupinus bicolor* (lupine), *Lupinus nanus* (sky lupine), *Triteleia laxa* (Ithuriel's spear) were all negatively associated with cattle grazing, while *Plagiobothrys nothofulvus (*popcorn flower) was positively correlated.



Appendix, Table 1. Sugar content (μg) per flower per species.

Genus_species	mean	SD	N
Acmispon_wrangelius	61.82	6.12	25
Acmispon_nevadensis_var_nevadensis	64.76	7.24	25
Allium_campanulatum	23.00	3.98	20
Clarkia_heterandra	18.35	6.57	10
Clarkia_unguiculata	20.60	7.02	20
Claytonia_rubra_ssp_rubra	9.48	3.52	20
Collinsia_childii	29.12	7.29	20
Collinsia_parviflora	26.44	5.98	20
Cryptantha_intermedia	24.86	4.09	20
Delphinium_patens	80.12	9.74	10
Dichelostemma_capitatum	74.83	10.56	20
Erysimum_capitatum	19.87	4.47	20
Erythranthe_sierrae	206.23	26.39	20
Gallium_aparine	2.58	0.41	20
Gayophytum_diffusum_subsp_parviflorum	9.48	3.52	20
Hosackia_crassifolia_var_crassifolia	13.32	3.11	20
Keckiella_breviflora	12.59	2.78	15
Leptosiphon_ciliatus	16.86	4.85	20
Nemophila_maculata	6.52	2.9	20
Penstemon_laetus	1032.41	40.23	15
Phacelia_douglasii	30.55	3.54	10
Prunus_virginiana_var_demissa	266.23	15.34	20
Ranunculus_californicus	49.33	7.18	15
Ribes_roezlii_var_roezlii	27.57	6.65	20
Symphoricarpos_mollis	74.35	8.73	20
Triteleia_ixioides	165.40	23.62	10
Triteleia_laxa	263.44	29.97	10

Appendix, Table 2. Statistical model structure and fitting.

Response variable	Explanatory factors	Candidate model structure	df	AICc
Total flowers	Null (block effect only)	1 + (1|site/block)	4	547.10
	Full (treatment, site, and their interaction)	treatment + site + treatment*site + (1|site/block)	12	536.53
	Treatment, site (no interaction)	treatment + site + (1|site/block)	8	541.05
	Treatment	treatment + (1|site/block)	6	543.01
	Site	site + (1|site/block)	6	545.92
Shannon index	Null (block effect only)	1 + (1|site/block)	4	-22.917
	Full (treatment, site, and their interaction)	treatment + site + treatment*site + (1|site/block)	12	9.601
	Treatment, site (no interaction)	treatment + site + (1|site/block)	8	-16.965
	Treatment	treatment + (1|site/block)	6	-18.988
	Site	site + (1|site/block)	6	-22.312
richness	Null (block effect only)	1 + (1|site/block)	4	130.733
	Full (treatment, site, and their interaction)	treatment + site + treatment*site + (1|site/block)	12	115.734
	Treatment, site (no interaction)	treatment + site + (1|site/block)	8	122.638
	Treatment	treatment + (1|site/block)	6	129.255
	Site	site + (1|site/block)	6	122.699
Total sucrose per .25 ha	Null (block effect only)	1 + (1|site/block)	4	734.832
	Full (treatment, site, and their interaction)	treatment + site + treatment*site + (1|site/block)	12	724.158
	Treatment, site (no interaction)	treatment + site + (1|site/block)	8	730.69
	Treatment	treatment + (1|site/block)	6	735.178

	Site	site + (1|site/block)	6	729.201

Appendix, Table 3. Final model terms, error structures, and marginal and conditional coefficients of determination (R2) for linear and generalized linear mixed effects models predicting floral resource components. Marginal and conditional coefficients of determination give the variance explained by all model terms (i.e., random and fixed effects) and the variance explained solely by the fixed effects, respectively.

Response	Final Model Structure	Error Structure	Marginal R2	Conditional R2
Total flowers	Total ~ treatment + treatment*site + (1|site/block)	Negative Binomial	0.854	0.854
Floral richness	Richness ~ treatment + treatment*site + (1|site/block)	Gaussian	0.899	0.959
Floral diversity-Shannon index	Shannon ~ site + (1|site/block)	Gaussian	0.980	0.988
Total nectar sugar per .25 ha	Sugar ~ treatment*site + (1|site/block)	Negative Binomial	0.200	0.205

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