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ARTICLE
Disease Ecology

Variable effects of wildlife and livestock on questing tick abundance across a topographical–climatic gradient

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Abstract

Large-bodied wild ungulates are declining worldwide, while domestic livestock continue to increase in abundance. Such changes in large herbivore communities should have strong effects on the control of ticks and tick-borne disease as they can indirectly modify habitat and directly serve as final hosts for ticks' lifecycles. Numerous studies have now linked changing ungulate communities to changes in tick populations and disease risk. However, the effects of changing large herbivore communities are variable across studies, and the effect of climate as a mediating factor of this variation remains poorly understood. Also, studies to date have largely focused on wildlife loss without considering the extent to which livestock additions may alter tick populations, even though livestock replacement of wildlife is the global norm. In this study, we used a large-scale exclosure experiment replicated along a topo-climatic gradient to examine the effects on tick populations of both large herbivore removal and livestock additions. We found that while questing ticks increased modestly, by 21%, when large herbivores were removed from a system they decreased more substantially, by 50%, when livestock (in the form of cattle) were added. Importantly, in addition to the direct effects of climate on tick populations, climate also mediates the effect of ungulates on questing tick density. Particularly, the addition of livestock under the most arid conditions decreased tick presence, likely due to changes in ground-level microclimates away from those beneficial to ticks. Overall, the work contributes to our understanding of tick population responses to globally common human-induced rangeland alterations under the concurrent effects of climate change.

KEYWORDS
California, climate, large herbivores, livestock, ticks, ungulates

INTRODUCTION

Wild ungulate herbivores are disappearing from many ecosystems worldwide through land-use changes and overexploitation, and ~60% of species are at risk of extinction (Ripple et al., 2015). However, defaunation is not occurring in isolation; typically, it occurs simultaneously with the introduction of domestic herbivores like cattle (Barnosky, 2008; Orr et al., 2022; Young et al., 2013) and concurrently with climate change (Dirzo et al., 2014; Young et al., 2016). Domestic livestock biomass is presently over 14 times that of large vertebrate wild animals (Bar-On et al., 2018). Cattle grazing impacts on vegetation have created immense and cascading effects on ecosystems, including changes in soil carbon storage (Forbes et al., 2019; Sitters et al., 2020) and landscape productivity (Charles et al., 2017; Travers et al., 2018), but these effects can differ based on environmental context, stocking density, and behavior among other factors (Veblen & Young, 2010; Young et al., 2013).

Notably, landscape effects of shifting herbivore communities can be altered by aridity and climate change. Grasslands, shrublands, and savannas are the predominant rangelands for many wild ungulates and most cattle. These dryland ecosystems (systems with aridity indexes of <0.65) compose 41% of the land surface and are inherently water-stressed systems (Gaur & Squires, 2018). As such, they are already predisposed to respond strongly to climate warming or drought conditions. Aridity has been well established to strongly mediate the cascading impact of large ungulate herbivores on plant communities by magnifying the effects of grazing stress on plant biomass, density, and diversity (Goheen et al., 2013; Orr et al., 2022; Pringle et al., 2007; Young et al., 2013).

Ungulate communities also strongly impact arthropod disease vectors such as ticks (family Ixodidae: subclass Acari) (Goheen et al., 2018; Keesing et al., 2013; Young et al., 2014). Many tick species rely on large herbivores, mammals, and reptiles as blood-meal hosts, requiring a blood meal for each life cycle stage. Host population size strongly impacted tick population abundance for tick species, *Ixodes ricinus* and *Ixodes pacificus* (Randolph, 2004; Swei et al., 2011). Ungulate herbivores—both wild and domestic—serve as final hosts for many tick species and can be necessary for certain tick species like *Ixodes scapularis*, *Amblyomma americanum*, *Rhipicephalus annulatus*, and *Haemaphysalis longicornis*, to reproduce and complete their life cycle (Tsao et al., 2021). Without their final hosts, ticks may not reproduce, and for *I. pacificus*, it was found that a loss of such hosts typically decreased their population sizes (Gilbert et al., 2012; Kilpatrick et al., 2014). However, the removal of large hosts can also cause increasing tick abundance through the competitive release of their juvenile-stage hosts, typically small vertebrates. In the Kenyan Long-term Exclosure Experiment (KLEE), plots manipulatively removing large herbivore wildlife resulted in a significant increase in small mammalian hosts seen by Young et al. (2014). This was postulated as enabling the response seen in Titcomb et al. (2017), wherein the same plots, abundance of ticks *Rhipicephalus pravus*, *praetextatus*, and *pulchellus* significantly increased. This variableness in tick response to host community change highlights the complexity of tick-to-host dynamics within landscapes and how multiple factors may interactively impact their landscape-level abundances.

Tick populations are also strongly impacted by environmental conditions, notably aridity, which is expected to develop in intensity under climate change. The timing of host-seeking behavior and abundance for *I. pacificus* changed with increasing aridity in different landscapes (Kilpatrick et al., 2017; MacDonald, 2018). In the Southwestern United States, increasingly hotter and drier summers have truncated their activity (MacDonald et al., 2020; MacDonald & Briggs, 2016). Local climatic conditions shape tick presence and survival, given that ticks spend ~90% of their lifecycle off-host and are sensitive to changes in temperature or humidity (Needham & Teel, 1991). In especially arid conditions, *Ixodes* spp. ticks escape to nearby moist microclimates, a defense from desiccation-related mortalities (Gray et al., 2016; Padgett & Lane, 2001). Herbivores themselves affected the microclimates available to *I. pacificus* and *Dermacentor variabilis* larvae at ground level through the grazing and trampling of vegetation and the grazing and compaction of soils (D. Orr et al., unpublished manuscript).

Reported tick-borne diseases were 77% of all reported vector-borne disease cases in the United States and are likely even in this statistic to be underreported as many cases go undiagnosed (Rosenberg, 2018). The Pacific coast tick (*Dermacentor occidentalis*) is a regionally common tick in the Southwestern United States and a vector of human pathogens *Rickettsia rickettsii* (Rocky Mountain spotted fever) and Rickettsia 364D. Additionally, they are vectors of livestock disease *Anaplasmosis bovis*, and *Ehrlichia chaffeensis* in both humans and livestock (Holden et al., 2003; Lane et al., 2010; Padgett et al., 2016). Given that ticks influence both human and livestock health, it is crucial to understand the fluctuations in ticks and tick-borne diseases that may occur as rangeland large herbivore communities' change.

Studies of tick responses to climatic context (Dantas-Torres, 2015; Eisen et al., 2002, 2016; Levi et al., 2015; MacDonald et al., 2020), native ungulate community alteration (Bloemer et al., 1986; Daniels et al., 1993; Gilbert et al., 2012), and in fewer cases, domestic livestock or cattle additions (Keesing et al., 2013; Mutizhe et al., 2021) have increased our understanding of tick populations in these anthropogenic rangeland landscapes. However, much more work needs to be done to investigate how these factors interact, as there is some strong evidence that this interaction can dampen or amplify tick responses (Keesing et al., 2018; Titcomb et al., 2017).

We address this challenge using a tightly controlled herbivore exclosure experiment in southern California, replicated across a climatic gradient. The study addresses three questions for this system: (1) What are the effects of total large herbivore removal and cattle addition on tick abundance? (2) How does tick abundance vary across climatic contexts? (3) Is there an interactive effect between either large herbivore loss or cattle addition and climate conditions? First, we hypothesized that large herbivore removal (simulating total defaunation) would result in an increase in tick abundance due to removing grazing pressure and increasing vegetative biomass that would create tick-beneficial microhabitats. Cattle additions, we expect, would cause a decrease in abundance with the loss of vegetation increasing the desiccation risk of ticks on the landscape. Additionally, we anticipate that increasing aridity of our climate levels would decrease tick abundance. Further, we expect that there would be an interactive effect between climate and herbivore exclusion treatment in predicting tick abundance. This interaction will cause the effects of cattle addition to be strongest in more arid conditions. Lastly, it is likely that tick responses to climate level and herbivore treatment will change throughout the years of our study due to the multi-year lifespan of ticks and the time it will take for the landscape vegetation to respond to our exclosure treatments.

MATERIALS AND METHODS

Study area

We conducted this study on Tejon Ranch in Kern County, CA (34°59′ N, 203118°43′ W). Tejon Ranch is a mixed–cattle ranch and wildlife conservation property containing 97,124 ha of conserved land. Wild ungulates on the ranch include populations of mule deer (*Odocoileus hemionus*), Rocky Mountain elk (*Cervus canadensis nelsoni*), feral pig (*Sus scrofa*), and pronghorn (*Antilocapra americana*), as well as livestock (black angus beef cattle) at an average stocking density of 0.13 head/ha which falls within the range of recommended stocking density for Sierra foothill and coast-range oak woodland landscapes (George et al., 2020). All plots were established in mixed oak savannah woodland. The study area is characterized by rugged topography creating steep aridity gradients, providing strong local variation in climate, and is projected to experience increased aridification under climate change over the next century (McCullough et al., 2016). The regional climate is Mediterranean, with hot, dry summers and cooler, wetter winters. Field collections for this study occurred between 2016 and 2019, during and directly after the California drought (~2011–2017), the driest period recorded in state history (Griffin & Anchukaitis, 2014; Mount et al., 2021).

We detected three tick species in this study: *D. occidentalis* (pacific coast tick, most collected), *I. pacificus* (black-legged tick), and *D. variabilis* (American dog tick). In southern California, *D. occidentalis* has been found to be tolerant of open, arid habitats (MacDonald, 2018), whereas *I. pacificus* is less tolerant and appears more in denser, cooler, forested-type habitats (Eisen et al., 2006; MacDonald, 2018). *D. variabilis* aridity tolerance and preference for more open habitats are like *D. occidentalis*, but it is found in greater abundance toward the California coast and is collected less frequently in the central/eastern part of the state (Furman & Loomis, 1984; Minigan et al., 2018).

In addition to the diseases of concern for human and animal health vectored by *D. occidentalis* (Rocky Mountain spotted fever, Ehrlichiosis, and Anaplasmosis), *I. pacificus* and *D. variabilis* are also known vectors of diseases. *I. pacificus* is the vector for the most common tick-borne disease, Lyme disease (*Borrelia burgdorferi*) (Lane et al., 2010; MacDonald et al., 2017), and another disease, tick-borne relapsing fever (*Borrelia miyamotoi*) (Sambado et al., 2020). *D. variabilis* is an additional vector of Rocky Mountain spotted fever (*R. rickettsii*) and tularemia (*Francisella tularensis*) (Minigan et al., 2018).

Experimental design

This work was conducted inside the Tejon Ranch Exclosure Experiment (TREE), an ongoing study utilizing a replicated system of three exclosure types to alter the presence of cattle and wild ungulates across three climate levels distinguished by topography (increasing elevation) and directional slope (southern and northern facing). TREE consists of twenty-seven 1-ha plots spanning these three climatic aridity levels, with nine plots at each grouped into three replicate blocks that contain one of each herbivory treatment exclosure (Figure 1a).

Categorization of climate levels

The climate levels for our experiment were established using available climate grids downscaled to 30 m

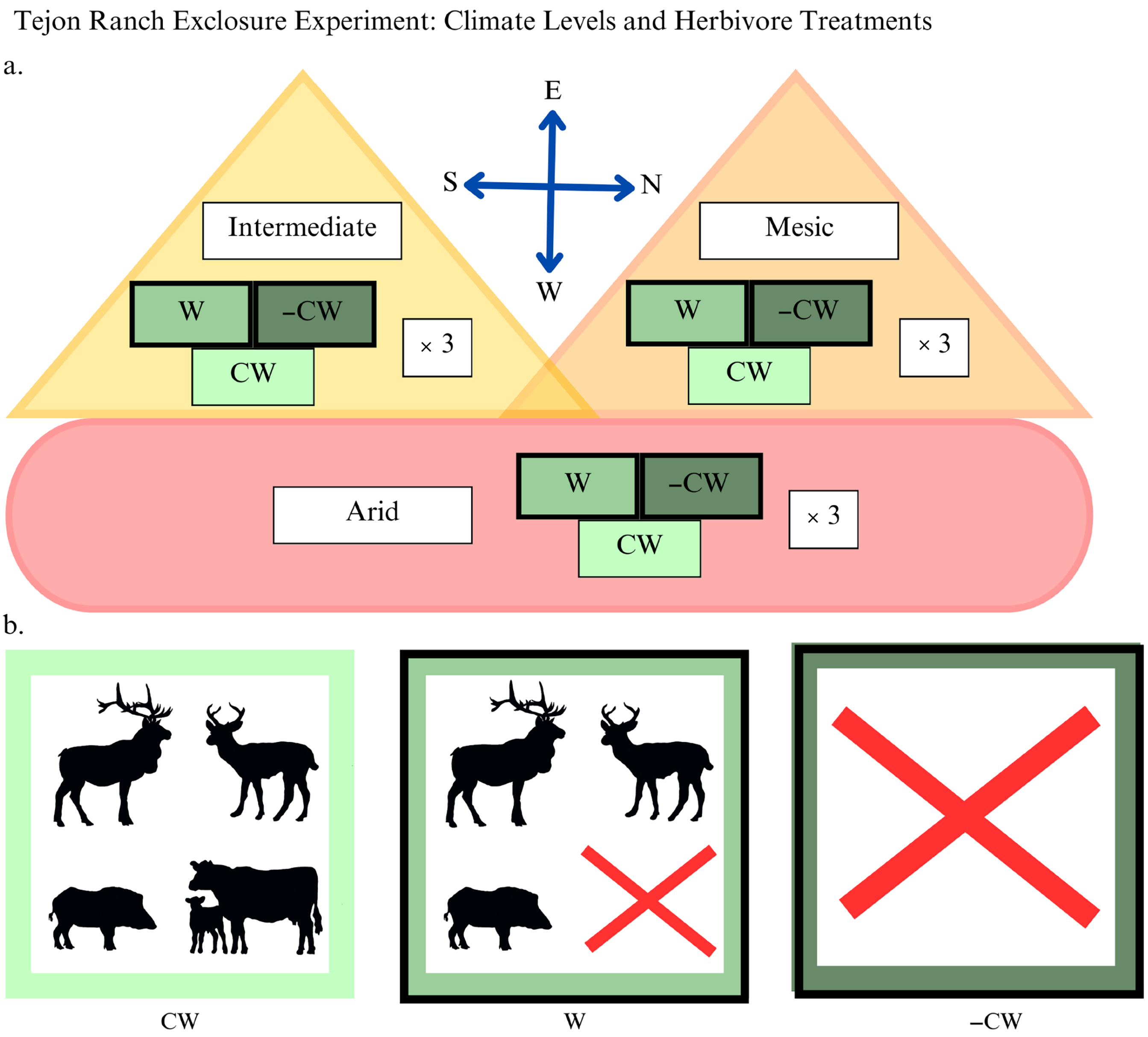

FIGURE 1 (a) The experimental design of the Tejon Ranch Exclosure Experiment (TREE). TREE consists of three distinct climate levels—Arid, Intermediate, and Mesic. The Arid-climate herbivore exclosures are at ~580 m in elevation. Intermediate and Mesic are at the same elevation level, ~1650 m, but are located on opposite-facing slopes; with Intermediate-level exclosures on the south-facing slope and the Mesic-level exclosures on the north-facing slope. At each climate level, a triplicate array of three large herbivore exclosure treatments was constructed. (b) Each replicate at a climate level includes one exclosure treatment functionally removing access of all large herbivores to the plot called *minus cattle and wildlife* (−CW) plot. A second exclosure treatment limits plot access to large wildlife herbivores only while preventing domestic herbivores access, called *wildlife* (W) plot. Finally, the *cattle and wildlife* (CW) plot has no exclusionary fencing and permits the access of both wild and domestic large herbivores. Both plots, W (*wildlife*) and −CW (*minus cattle and wildlife*), were created with barbed-wire fencing and, in the figure, have thick black borders whereas the non-fenced herbivore treatment, CW (*cattle and wildlife*), has no black border.

(Davis & Sweet, 2012; McCullough et al., 2016). Each climate level is separated by approximately 2°C average temperature and 200–300 mm annual precipitation (Orr et al., 2022). Additionally, all climate levels differed significantly in daily maximum and daily minimum temperatures (Klope, 2021). The three climate levels in TREE are Arid, Intermediate, and Mesic. Arid is the hottest and driest level, followed by Intermediate; Mesic is the coolest and wettest level (Figure 1a). The locations were selected to approximate present, near future, and far future climate scenarios (Orr et al., 2022).

Herbivory treatments

The three herbivore exclusion treatments consist of *wildlife* (W) (simulating conserved conditions for the landscape), *cattle and wildlife* (CW) (simulating typical ranching conditions in the area), and *minus cattle and wildlife* (−CW) (simulating defaunation) (Figure 1b). *Wildlife* exclosures use semipermeable barbed wire fencing to remove livestock but allow wildlife access. *Cattle and wildlife* exclosures have no fencing and t-posts demarcating plot corners. *Minus cattle and wildlife* exclosures were constructed with complete barriers of barbed wire fencing, which functionally excluded large herbivores over 40 kg in body mass (Figure 1b). Exclosure fencing for the herbivory treatments was established in November 2016, and monitoring of dung counts across all plots confirmed that treatments operated as intended (Orr et al., 2022).

Tick sampling

We evaluated tick populations by sampling questing ticks in the plots before the herbivore exclusion treatments were applied (April–December 2016) and for the first 3 years of the experiment post-exclusion treatment implementation (2017–2019). Each plot was sampled for ticks by dragging a 1-m^2 white flannel cloth through the understory for 1 h with the drag cloth being checked by the sampler for attached ticks every 80 m, or approximately every 1–3 min. All herbivore treatment plots were sampled at least monthly from 2017 to 2019 (except for October 2019). In 2017 and 2018 during the month of April, the treatment plots were dragged for two additional 60-min periods, and in May, the plots were dragged for an additional 60-min period. In 2019, all treatment plots were sampled for an additional 60-min drag in April and in June. In the month of May, the herbivore treatments at the Intermediate and Mesic climate levels were sampled an additional time, whereas the plots at Arid were only sampled once. The data from each 60-min drag were not aggregated by month and remained a separate sampling period within the dataset and subsequent analyses. This metric of adult ticks/hour establishes plot relative tick abundance, where the rate of collection is a proxy metric for the true abundance of adult ticks within the plot. The herbivore exclosures were only sampled on days when the temperature was above 10°C, and there was no rain or low fog, strong wind, or snow. Any ticks found on the cloth within the 60-min sample period were collected with tweezers and stored in 70% ethanol. Ticks were identified to species in the field, and if further confirmation was needed, they were taken back to the laboratory for further examination under a dissection microscope.

DATA ANALYSES

Questing tick density

Statistical analyses focused on questing *D. occidentalis* collected from hour-long cloth drag efforts, that occurred monthly from 2017 through 2019, encompassing the 3-year period post-exclosure construction. Since the relative abundance of *I. pacificus* and *D. variabilis* were low, tick totals of all species (*I. pacificus*, *D. occidentalis*, *D. variabilis*) were combined in the summary analysis, but only *D. occidentalis*, the species most collected within our study, was used for the effect and regression analyses. Despite extensive efforts to collect the juvenile life stages of all tick species, we had limited success, and therefore, only the adult life stages were included in the analysis. Our collected data were non-normal and therefore necessitated the use of nonparametric tests and a generalized mixed linear model with a negative binomial distribution for model analyses. All analyses were performed within various statistical packages in RStudio (v 4.4.1).

Tick density relationships with herbivores and climate

Effect size

To measure the strength of the relationship between herbivore treatment and climate levels on relative *D. occidentalis* abundance, we calculated the effect size using a nonparametric Kruskal–Wallis test followed by a post hoc Dunn's test with a Bonferroni correction.

Incorporating interactive context between herbivore exclusion and climate

Model construction

Using adult *D. occidentalis*/hour as the response variable, we fit generalized linear mixed models (GLMMs) with a negative binomial distribution. We included the fixed effects of herbivore treatment (−CW, W, CW), climate (Arid, Intermediate, Mesic), and then year (2017, 2018, 2019). Year constitutes as a proxy for how many years exclosure fences have been constructed. The model intercept was set to W exclosure treatments at climate level Intermediate and represents mid-level aridity between Mesic (wetter) and Arid (drier). The herbivore exclosure type, W, represents the landscape before the addition of domestic livestock in the CW treatments and represents the landscape not affected by the total defaunation of our −CW treatments. Therefore, as the intermediary exclosure type, it is used as our model intercept. Our models' random effects accounted for the non-independence of repeated sampling of plots over time and tick seasonality. Therefore, we included a unique plot ID to represent each of the 27 plots on an individual basis and month due to the natural seasonal variation of tick populations. All models were constructed using the "glmmTMB" package and glmmTMB() function (Brooks et al., 2017).

Model comparisons and assessments

We compared candidate models using model Akaike information criterion (AIC) values and one-sided likelihood-ratio tests with the anova() function. For our best-fit model, we compared marginal and conditional R^2 to explore the importance of fixed and random effects in accounting for the observed variation in relative *D. occidentalis* abundance. Finally, we used k-fold cross-validation using the "caret" package and modeled predicted versus observed values to determine the overall success of model fit (Kuhn, 2008).

RESULTS

Questing ticks varied by herbivore exclosure type and topo-climate level

Tick sampling from 2016 to 2019 resulted in the collection of 2692 questing adult ticks. The most common tick species collected via tick drag was *D. occidentalis* ($n = 2420$, 89.9%), then *I. pacificus* ($n = 206$, 7.7%), and lastly *D. variabilis* ($n = 68$, 2.5%). When comparing mean tick collection per hour rates of all three tick species collected across herbivory treatments, −CW (*minus cattle and wildlife*) plots had the highest relative abundance ($u = 3.2 \pm 6.4$ ticks/h, mean ± SD), followed by W (*wildlife*) ($u = 2.2 \pm 5.1$ ticks/h) and then CW (*cattle and wildlife*) ($u = 1.2 \pm 3.2$ ticks/h). Mean relative abundance of adult ticks by climate level were highest in Intermediate ($u = 3.7 \pm 7.0$ ticks/h), followed by Mesic ($u = 1.3 \pm 2.2$ ticks/h) and Arid ($u = 0.76 \pm 2.8$ ticks/h).

Relative *D. occidentalis* abundance was significantly different between herbivore exclosure treatment and climatic level

Adult *D. occidentalis*/hour was significantly different between the herbivory treatments ($p < 0.001$) and climate levels ($p < 0.001$). For herbivore exclosures, it was significantly different when comparing CW exclosures with W exclosures ($p < 0.001$) or when comparing CW exclosures with −CW exclosures ($p < 0.001$). There was no significant difference in relative *D. occidentalis* abundance between the W and −CW exclosures ($p = 0.36$; Figure 2a). Adult *D. occidentalis*/hour was significantly different between all three climate levels (Figure 2b). The effect of climate level on relative *D. occidentalis* abundance based on the Kruskal effect size was moderate (H-statistic = 0.060). It was greater than the effect of herbivore treatment on relative *D. occidentalis* abundance, which was small (H-statistic = 0.012).

There was a significant interaction between herbivore exclosure and climate level

Our best-fit model included a three-way interactive term between our fixed-effects herbivory treatment, climate level, and year (df = 30). The fixed effects accounted for a small proportion of the variance (marginal $R^2 = 0.15$) but including the random effects of month and plot ID improved model fit (conditional $R^2 = 0.90$). Nonetheless, including fixed effects improved the model fit more than the null model without fixed effects (McFadden's $R^2 = 0.22$). We found that the interaction between CW plots and the Arid climate level was significantly different than that of the model intercept ($p = 0.02$). The CW plots at Arid were predicted to have approximately two fewer *D. occidentalis* adult ticks per hour collection period (estimate $= -2.1 \pm 0.9$). Regardless of herbivore treatment, the Arid climate level was predicted to have approximately one less questing *D. occidentalis* adult tick per hour collection period than the model intercept ($p = 0.005$, estimate $= -1.4 \pm 0.5$). Except in 2019, when this trend reversed, and it predicted there would be more questing *D. occidentalis* adults at the Arid climate level ($p < 0.001$, estimate $= 1.4 \pm 0.4$). The only other predicted significant interannual variation also occurred in 2019, where, during this year, the −CW plots were predicted to have fewer questing *D. occidentalis* adults per hour ($p = 0.05$, estimate $= -0.7 \pm 0.3$; Figure 3; Table 1; Appendix S1: Table S1).

Model fit was likely impacted by the variance of questing *D. occidentalis* within the herbivore treatment

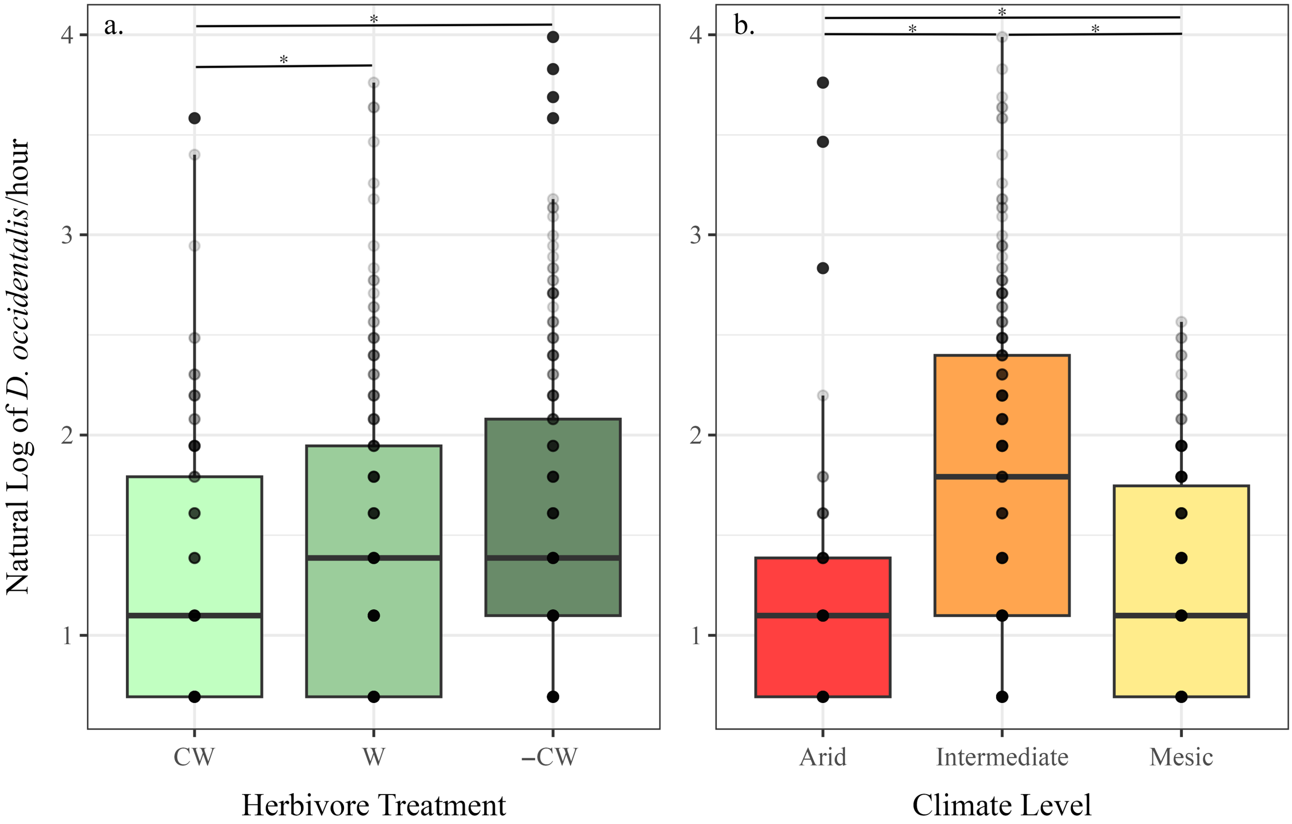

FIGURE 2 (a) The log-transformed relative abundance of adult *Dermacentor occidentalis* across the experimental herbivore treatments. There was a significant difference in relative abundance between the CW (*cattle and wildlife*) plots and the −CW (*minus cattle and wildlife*) plots. Additionally, there was a significant difference in *D. occidentalis* abundance between the CW and the W (*wildlife*) plots. There were no significant differences in relative *D. occidentalis* abundance between the W and −CW exclosure treatments. (b) Relative *D. occidentalis* abundance was significantly different across all three climate levels. The Intermediate climate level had the highest relative abundance of questing *D. occidentalis* whereas the Arid climate level had the lowest abundance. In (a) and (b), the horizontal black line with an asterisk above between the bar plots denotes a significant difference. The black midline within the boxplots is the median whereas the color outline of each box plot signifies the upper a lower quantiles, the whiskers show the maximum and minimum values of the data that are not outliers. Data points above the whiskers are considered to be outliers or at least occassions when tick counts were particularly high for the treatment type even under a natural log transformation. The other black points that fall within the boxplot and its whiskers are also log scaled data points of the tick counts by treatment type.

plots. The relative *D. occidentalis* abundances we collected showed that 1.74% fell three SDs above the mean (standardized residuals: $u = 0$, $\mathrm{SD} = 1$). Yet, a k-fold ($k = 15$) cross-validation showed relatively stable model performance across folds. Additionally, the predicted model means fit well to the observed means of herbivory treatment and climate level; averaging dampened the effect of this variation (Appendix S1: Figure S1a,b).

DISCUSSION

Our study explored the effects of changing large herbivore communities on questing adult ticks, particularly the tick species, *D. occidentalis*, and its mediation by topo-climatic context. This was further affected by temporal scales (months within a year and across 3 years) (Figure 3; Appendix S1: Figure S2). Both herbivore treatments and climate levels influenced relative *D. occidentalis* abundance, but climate had a greater effect. Yet, the presence of cattle on the landscape further decreased the adult *D. occidentalis* abundance than climate alone. This was especially pronounced under the most arid conditions of our study.

Our results confirm our hypotheses and supports previous work under similar experimental conditions from Kenya (Titcomb et al., 2017). Titcomb et al., at the Ungulate Herbivory Under Rainfall Uncertainty (UHURU) experiment, found a significant interaction between their experiment's total large herbivore removal (a version of −CW exclosures) and climate level (delineated by differences in mean annual precipitation). Their work found an increase in tick abundances within their −CW exclosures at their most arid location (Titcomb et al., 2017). Our study also found a significant interactive effect of climate level and herbivore treatment at our

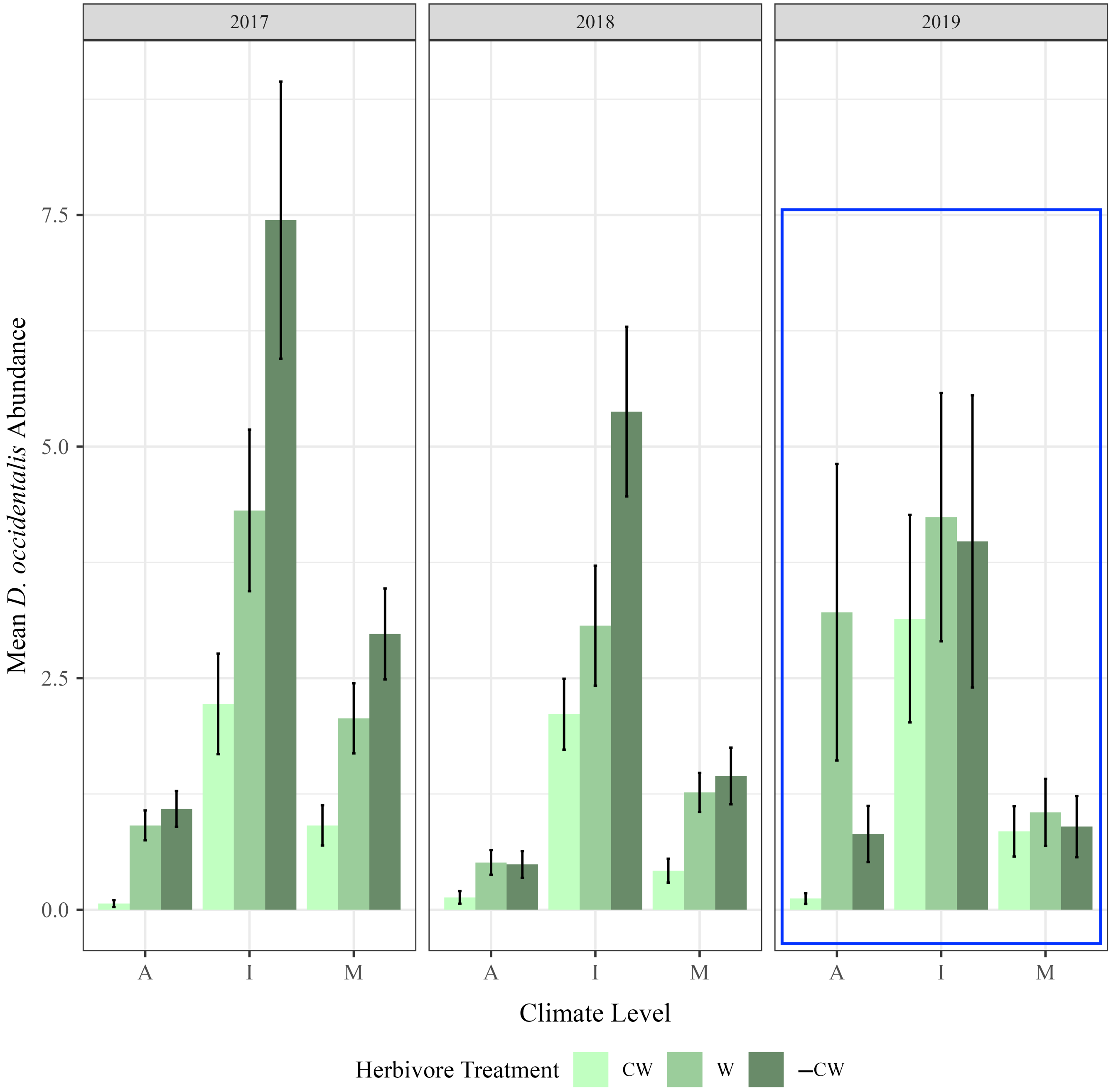

FIGURE 3 Yearly relative *Dermacentor occidentalis* abundance for the years post-exclosure installation, 2017–2019 (mean ± SE) for climate level: Arid (A), Intermediate (I), and Mesic (M) and herbivore treatment type: CW (*cattle and wildlife*), W (*wildlife*), and −CW (*minus cattle and wildlife*). In 2017 and 2018, the average *D. occidentalis*/hour was highest in the −CW (*minus cattle and wildlife*) exclosures. In 2019, the highest average relative abundance by exclosure treatment changed to the W (*wildlife*) exclosures, highlighted by the blue box in the figure. There was a particularly large relative abundance change between exclosure treatments at the Arid climate level.

most arid study location. But opposite of Titcomb et al., our interaction was between our open CW (*cattle and wildlife*) plots and resulted in a decrease in relative *D. occidentalis* abundances to their lowest levels (Table 1). Within our study questing adult ticks and relative *D. occidentalis* abundance were highest within the −CW plots at the Intermediate climate (Figure 2a,b), differing from the results determined in Kenya.

Our similar and differing results to Titcomb et al. (2017) suggest that the way managerial entities of rangelands deal with tick presence and tick-borne disease risk will be highly context-dependent, with the life cycle, life history traits, and climatic resiliency of ticks varying greatly across global rangeland regions even under similar climate aridity regimes. Climate becomes more significant to population success toward the end of range

TABLE 1 The significant results from the best-fit generalized mixed linear model—*Dermacentor occidentalis* ~ herbivory treatment × climate level × year + (1|Month) (1|PlotID)—with a negative binomial transformation.

Outputs	Estimate	SE	z	p
Model intercept	−0.27	0.78	−0.34	0.73
Arid	−1.38	0.49	−2.80	0.005
CW:Arid	−2.08	0.90	−2.31	0.02
−CW:2019	−0.66	0.33	−1.99	0.05
Arid:2019	1.35	0.39	3.42	0.0004

Note: The model resulted in an Akaike information criterion (AIC) value of 3088.4, Bayesian Information Criteria of 3239.9, and a log likelihood value of −1514.2. Conditional R^2 for the model was 0.90 whereas the marginal R^2 and the McFadden's R^2 were lower at 0.15 and 0.22, respectively. There was a predicted significant interactive effect ($\alpha \leq 0.05$) of herbivory treatment and climate level at the Arid climate and separately within the CW (*cattle and wildlife*) treatment plots at the Arid climate across experiment years. Additionally, there was a predicted significant change in *D. occidentalis* responses within the −CW (*minus cattle and wildlife*) exclosure plots as well as at the Arid climate level in the year 2019. A full model summary is available in Appendix S1: Table S1.

limits than it does to populations at the center of species ranges (Hampe & Petit, 2005; Thomas, 2010). This likely explains the significance of climate level in our system. The climate levels are established by topography that creates cooler and moister environments higher in elevation than at the valley floor. The questing ticks at lower elevations deal with increased climate-related stress than those at higher elevations, reducing their overall relative abundance (Figure 2a). Under climate change scenarios, it is predicted that areas at higher elevations will experience increased temperatures (Pepin et al., 2015). *D. occidentalis* abundance will potentially decrease on this landscape with the continued temperature rise and increased aridity under the current projections for climate change in the area.

Protection from climatic stress for tick populations comes from seeking microclimate refugia within the landscape. Inside our herbivore exclosure treatments, the mechanism most likely related to tick population success is the change in microhabitat conditions that improved tick survival. Microclimate refugia have been found to protect tick populations from otherwise fatal climatic conditions (e.g., soil to protect from wildfire and snow to insulate from below-freezing temperatures) (MacDonald, 2018; Padgett et al., 2009; Volk et al., 2022). All tick stages are particularly sensitive to aridity and the risk of desiccation when not on a host (Bouchard et al., 2019; Needham & Teel, 1991).

In 2019, Orr et al. (2022), at TREE, evaluated the impact of climate and herbivore treatment on plant community structure by sampling thirty-six 1 m × 1 m subplots in each exclosure. Surveys of these 1 m × 1 m subplots included total vegetation cover, litter volume, and bare ground. Additionally, ΔPAR (photosynthetically active radiation) was used to determine the percent of light reaching the soil surface at 10 subplots per exclosure. Finally, 0.25 m × 0.25 m of residual dry matter (RDM) biomass was collected, dried, and weighed from each of the 36 subplots in each exclosure. Orr et al. found significant differences in all metrics between the −CW plots and the W and CW plots, except for total cover at the Intermediate climate level and total bare ground at the Mesic climate level. The addition of cattle also decreased shading in the CW plots, allowing more sunlight to reach the soil surface. These results indicate that the herbivore treatments, −CW and W, had significantly more vegetation cover than the CW plots. This additional vegetation likely provided the in-exclosure tick populations with the microclimate refugia needed for their survival within our study system.

Increased vegetation density from decreased grazing pressure in this system and in others increases plant biomass, lowers soil and aboveground temperatures, and increases humidity levels, all of which are beneficial to tick questing activity by lowering the risk of desiccation (Diuk-Wasser et al., 2021; Eisen et al., 2016; MacDonald, 2018). Tick abundance has increased in more temperate and moister areas (Eisen et al., 2016; MacDonald, 2018; Ogden & Lindsay, 2016). Cattle additions on the landscape increased herbivore biomass and grazing pressure and, therefore, decreased these tick-advantageous conditions.

Also at TREE, D. A. Orr et al. (unpublished manuscript), completed an in situ survivorship study on juvenile *I. pacificus* and *D. variabilis* ticks. For this work they additionally measured daytime soil temperature and relative surface humidity. They found soil surface temperature was significantly hotter in the less vegetation-dense CW plots and found that soil humidity was significantly different between the CW and W, −CW plots at the Arid climate level. Orr et al. concluded that large herbivores, particularly the addition of cattle, were drivers of microclimate change and best explained the results of their survivorship study. They found aridity, directly in climate and indirectly in grazing pressure, decreased the survival of tick juvenile life stages (larvae and nymphs) (Orr et al., unpublished manuscript). The results of Orr et al., finding the lowest survival rates in the CW treatments at the Arid climate level, help confirm our results. The less juveniles that survive on the landscape mean there will be less questing adult ticks on the landscape. The loss of microhabitat within this treatment likely limited tick survival and therefore abundance.

It is likely that our study, in sampling 3 years post-exclosure treatment installation, captured residual pre-exclosure ticks in our plots because of their approximately 3-year-long life cycle (Padgett & Lane, 2001), and the removal of final hosts with exclosure construction kept them questing on the landscape and therefore collected by our drag cloths (Rand et al., 2004). In the last year of the study (2019), there was a change in relative adult tick abundance between exclosure types. In 2017 and 2018, the −CW exclosures contained the highest numbers of adult ticks and in 2019, the greatest numbers of adult *D. occidentalis* collected via 1-h cloth drags, were inside the W exclosures (Figure 3). Our model also predicted this change, where in 2019, it expected there to be significantly less questing *D. occidentalis* adults in the −CW than in the W exclosures (Table 1). This change in relative abundance between exclosure type and the predicted significance of this treatment type highlights the importance of large herbivores as hosts for the continuation of tick populations. Large herbivores are typically parasitized by adult ticks and are also where the adult ticks breed (Bouchard et al., 2019; Kilpatrick et al., 2017). The full loss of critical final hosts results in the decrease of subsequent generations when questing adults cannot parasitize a final host and successfully mate. Further sampling within TREE is needed to confirm the change in relative *D. occidentalis* abundance from −CW to W exclosures as a result of wild herbivore presence perpetuating plot-level tick populations and not just an effect of inter-annual variation or another factor not included in this study.

Another mechanism suggested by Esser et al. (2018), as well as Buck and Perkins (2018), postulated that tick increases might be an artifact of experimental plot sizes and that in the absence of reproductive (large mammal) hosts, ticks might have dispersed in the exclosure plots via rodent populations (Buck & Perkins, 2018; Esser et al., 2018). These mechanisms and their impacts on tick abundance inside experimental plots do not fully explain our results. They would require very large numbers of plot-crossing or existing rodents and/or very high tick densities per animal. We sampled lizard and small mammal populations in all our plots and produced overall low capture rates (see Appendix S1). However, our study did not account for plot-crossing medium-sized mammals such as hares, sciurids, and small carnivores. *D. occidentalis* will parasitize mammals other than large herbivores as a final reproductive host (Lane et al., 2010; Padgett et al., 2016). We believe part of the remaining tick proliferation in −CW exclosures was due to present and passing medium mammalian wildlife that could still access these plots. To understand such impacts, focused sampling on these species is still needed within our system.

Other mechanisms have been proposed to explain the effects of large herbivores on ticks. In another study, cattle presence directly decreased tick populations. In Keesing et al. (2013), cattle acted as a final host sink for tick populations resulting from the routine application of acaricide to the cattle present (Keesing et al., 2013). The cattle present in our landscape are treated once yearly with acaricide during the winter or early spring (D. Orr, personal observation) before the seasonal period of peak tick questing activity. In our study, this is likely a compounding effect to the presence of cattle reducing vegetation cover and limiting off-host survival. Acaricide treatment would decrease on-host survival, killing attaching adult ticks for the period that the treatment is active (Petney & Horak, 1987; Walker et al., 2014). With the cattle treated once a year, it was undetermined how long the acaricide lasts and whether it would protect the cattle from tick attachment for the duration of the spring tick questing season or from the fall questing season, a smaller but nonetheless peak in tick host-searching activity that occurs before the winter months (Appendix S1: Figure S2). The cattle of the Tejon Ranch are very free-range, so regular application of acaricide is likely logistically infeasible for the livestock managers. Therefore, while this is likely a component of our study results, its significance remains unclear.

CONCLUSION

Our work demonstrates the significant potential of increasing climate aridity to alter tick populations, an effect notably exacerbated by landscape-level herbivory. While herbivore treatment was consistently incorporated in best-fit models for tick abundance, climate level was a stronger predictor when evaluated independently. Aridity will continue to impact landscape suitability for microclimates conducive to tick populations. Under climate change projections, Southern California and other parts of the globe are likely to have further reduced moisture, increasing temperatures, and are likely to see further reductions in tick populations. However, other geographic areas may see differing results of climate change, and the interactive impact of climate and herbivore biomass may be notably different on tick abundances in these locations. This highlights the need for studies to continue incorporating multiple drivers of tick abundances into analyses to further our understanding of the variability to tick populations under the effects of landscape alteration and climate change.

AUTHOR CONTRIBUTIONS

Devyn Orr, Hillary S. Young, and Andrea Swei conceived the project ideas, instituted the methodologies, and received funding for this work. Devyn Orr, An Bui, and Stephanie Copeland collected field data. Samantha Sambado analyzed the data and created manuscript figures. Stephanie Copeland was the lead writer and editor of the manuscript. All authors contributed reviews and feedback on drafts and have approved the publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data, data analyses, code, and figures (Copeland et al., 2025) are available from Dryad: https://doi.org/10.25349/D9M31J.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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