

WORKING TITLE: Context-dependent effects of wildlife declines and livestock additions on tick abundance in southern California

TARGET JOURNAL: Ecology; Proc B;; ?

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KEYWORDS: ticks, ungulates, livestock, zoonotic disease, context-dependence, California

POSSIBLE FIGURES:

Fig 1- overview of experiment

Fig 2- veg differences & conceptual diagram

Fig 3 – 2 plots: tick means vs plot types; ticks vs site types

Fig 4- bivariate: climate*treatment

Fig 5- plot for each of the 3 sites with diff in mean temp

Fig 6- vertebrate communities (either by plot or site type or ?)

Fig 7- GLMM table and maybe effects plots

Take-away conceptual diagram?

ABSTRACT: [ecosystem structure & function] Populations of large-bodied ungulate herbivores are shifting around the world, with cascading effects on ecosystem structure and function. One such function critical to the health of humans, livestock and wildlife is control of ticks and tickborne disease. Directly, large wildlife can serve as hosts for ticks, maintaining disease transmission cycles. However indirectly, they can modify habitat and suppress abundance of intermediate hosts, which in turn suppresses tick densities, thereby decreasing disease risk. While numerous studies have attempted to link wildlife loss to changes in tick populations and disease risk, most have been done at small spatial scales. Those limitations may inadequately capture indirect pathways, especially when measuring the effect of climate which can strongly mediate the effects of wildlife on plants and other taxa. Furthermore, wildlife losses are frequently accompanied by livestock additions; however, the degree to which livestock addition may alter transmission cycles remains largely unexplored. To address these gaps, we used a large-scale exclosure experiment replicated along a topoclimate gradient to empirically examine the effects of large wildlife removal and cattle additions on ticks and tickborne disease transmission dynamics under varying climatic conditions in southern California. We found that overall, questing tick abundance increases when wild herbivores are removed from a system, and decreases when livestock are added. Importantly, in addition to direct effects of climate on tick abundance, climate also mediates the effect of ungulates on questing tick density. Overall, this work advances our understanding of tick-borne disease transmission in the far western U.S. and the nuances of large-bodied host manipulation as a disease mitigation strategy.

INTRODUCTION

Anthropogenic change occurs globally across ecosystems (Dirzo et al., 2014; Gottdenker et al., 2014). These direct and indirect impacts can be profound, with implications for community structure and ecosystem functions which are becoming more challenging to investigate singular questions (Dirzo et al., 2014; Goheen et al., 2013). Direct anthropogenic impacts typically occur as landscape alterations such as deforestation or urbanization which increases habitat fragmentation, agricultural pressure, rangeland expansion, and resource extraction of land and water (Dirzo et al., 2014; Gottdenker et al., 2014; Myers et al., 2013; H. S. Young et al., 2013). Indirect impacts via climate change can result in sea-level rise, change of intensity and scale of extreme weather events and increasing global temperatures (Carvalho et al., 2017; Chapman et al., 2005; Gilbert, 2021; Goheen et al., 2013; Lafferty, 2009; Martens et al., 1995). Both direct and indirect impacts can cause downstream effects that impact community structure and ecosystem function and must be incorporated into ecological analyses for ecosystem management strategies (Chapman et al., 2005; Gottdenker et al., 2014; LoGiudice et al., 2003, 2008).

One prominent form of anthropogenic perturbation globally impacting ecosystems is defaunation (Dirzo et al., 2014; Goheen et al., 2013; McCauley et al., 2008; Pringle et al., 2006; H. S. Young et al., 2013). 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). However, defaunation is not occurring wholly in isolation, often simultaneously occurring with the introduction of other large herbivores, predominantly as livestock (Barnosky 2008; Knapp et al 1999; Milchunas, Sala & Lauenroth, 1988; Wardle, Barker, Yeates & Bonner 2001). Livestock may replicate native herbivory effects on vegetation yet there may be significant differences instead due to diet and behavior or densities on the landscape. High stocking densities of livestock, especially in low-productivity landscapes, have negatively impacted plant species' diversity and richness (Jeddi & Chaieb, 2010; Karami et al., 2019; Rickart et al., 2013; Schieltz & Rubenstein, 2016; H. S. Young et al., 2013; Zhao et al., 2005). Landscapes with additional stressors, such as arid climates, may experience increased degradation and result in desertification (Jeddi & Chaieb, 2010; Zhao et al., 2005).

Continuing responses to this change in herbivory pressure occur in top-down and bottom-up scenarios (Pringle et al., 2006; Torre et al., 2007; T. P. Young et al., 2010). A bottom-up development to grazing intensity is particularly evident for smaller vertebrate species within these rangeland landscapes (Haby & Brandle, 2018; Torre et al., 2007). Small mammalian communities may be altered in the presence of large herbivore communities, potentially due to the intensive grazing by livestock which alters vegetation abundance and diversity, creating a lack of available food, shelter, and resources, resulting in a decrease in small mammal abundances (Schieltz & Rubenstein, 2016). The opposite effect has been shown to occur where small mammal populations increase when grazing pressure of large herbivores are removed (Keesing et al., 2013; McCauley et al., 2008; H. S. Young et al., 2014).

Outside of mammalian vertebrates, large herbivory pressure has created noted effects on reptile squamate populations (McCauley et al., 2006). Like small vertebrates, the impact of livestock

grazing on reptiles includes a myriad of negative and positive results on reptile presence, richness, and abundance. The effects seem to link with species habitat and microclimate preference closely (Doherty et al., 2020; Neilly et al., 2021; Pringle et al., 2006; Read & Cunningham, 2010). Intense grazing and canopy removal may benefit some reptile species yet negatively impact others (Neilly et al., 2021). The creation or removal of microclimates via grazing may be more significant to reptiles than small mammals due to their ectothermic characteristics (Doherty et al., 2020).

One critical and often overlooked facet of anthropogenic change via defaunation and rangeland expansion is its impacts on arthropod vectors. Several tick (family Acari) species utilize small mammals and reptiles as blood-meal hosts. Ticks rely on a blood meal to perpetuate each molting stage in their life cycle, making host densities and populations critical to tick population success (Couper et al., 2020; LoGiudice et al., 2003, 2008; Salkeld & Lane, 2010). Changes in host populations via livestock intensity will have a direct impact on these external blood parasites (Keesing et al., 2013; Mutizhe et al., 2021; Titcomb et al., 2017). Ticks transmit a large portion of emerging vector-borne diseases, and in the United States (US), ticks are the most common vector of zoonotic diseases (Swei 2020, Rosenberg 2018). In the US, reported tick-borne diseases have doubled in the past decade, and in 2020, 40,000 cases of Lyme disease were reported (Kugeler 2021). Because ticks affect the well-being of humans, livestock, and wildlife, predicting where and when ticks and tick-borne diseases (TBDs) will be most prevalent under anthropogenic perturbation is a critical challenge.

Wildlife declines can directly affect tick abundance through the loss of hosts (Wilson et al. 1995; Perkins 2013). Specific studies have attempted to link wildlife loss to changes in tick-borne zoonoses, notably the removal of deer and the subsequent effect on Lyme disease prevalence (**Sources Needed**). Results are mixed, ranging from positive to negative to neutral (Perkins et al., 2013). Wild ungulate herbivores serve as final hosts for many tick species and are necessary for ticks to reproduce and complete their life cycle. But large ungulate wildlife can also indirectly affect tick survival and questing behavior by altering the abundance and composition of small vertebrate hosts (Keesing et al., 2013; Titcomb et al., 2017) (**Other sources?**). Large mammal loss often accompanies small mammal abundance increases (Mills 2006; Goheen 2013; Young et al. 2015), leading to changes in host availability for different tick species. Large mammal loss also impacts vegetation structure, affecting ticks during the off-host periods in their life cycles and potentially leading to increased desiccation (Civitello 2008; Randolph 2000; MacDonald 2018; Goheen et al. 2013; Bakker et al. 2006; Young et al. 2013).

Defaunation and subsequent rangeland expansion occurs concurrently with the global effects of climate change, complicating ecological investigations. Prior studies have demonstrated that the functional roles of large ungulate wildlife are highly dependent on climatic context, which often mediates the strength or outcome of their interactions in a community (Rickart et al., 2013; Rotem et al., 2015; Zhao et al., 2005). It is now clear that abiotic site characteristics (e.g., vegetation productivity, climatic conditions) can strongly mediate the impact of large ungulate herbivores on plant communities (Augustine & McNaughton, 2006; Bakker et al., 2006; Borer et al.). Likewise, the indirect effects of large herbivores on other small consumers, from insects to birds and small mammals, are susceptible to variation in climate and productivity (Daskin & Pringle 2016). Still, it is unclear whether these results can be generalized to tick abundance.

Ticks spend ~95% of their lifecycle off-host, making local climatic conditions imperative to their presence and survival (G R Needham & Teel, 1991). Hard-bodied, Ixodidae ticks are Holarctic arthropod vectors that are highly associated with environments that retain ample ambient moisture (**Sources Needed**). Climate change has been shown to alter host seeking behavior (i.e., tick phenology) and abundance in different landscapes. As ectotherms, ticks are sensitive to changes in temperature and humidity which have become indices for their population demographics. In the northeastern US, shorter mild winters and longer humid summers have increased the length of host-seeking tick activity (**Levi & Ostfeld**). In the far western US, increasingly hotter and drier summers have truncated tick activity (**pub. by Dr. MacDonald**), especially compared to the northeast (-> **description more resembles PNW**), wherein tick activity can continue year-round in certain areas.

Tick-borne diseases present an increasing risk to human, domestic, and wildlife health with continued global anthropogenic change (Jones et al., 2008; Daszak et al., 2000). Understanding the ramifications of the interactive effects of large herbivore assemblages with climatic change requires empirical investigation into these impacts on tick abundances, a need highlighted by recent studies (e.g., Titcomb et al. 2017; Keesing et al. 2013). There have been manipulative experiments on wild ungulate loss to tick abundances (**Sources Needed**). Others have included or have singularly investigated domestic herbivore presence (**Sources Needed**). Finally, others have investigated a climatic gradient narrative through tick abundances across elevational change or precipitation gradients (**Sources Needed**). These studies are beneficial to understanding the disparate effects of climate and large herbivores on tick populations. Yet, they have highlighted a knowledge gap in the lack of empirical studies examining how multiple simultaneous forms of human perturbation may interactively drive both direct and indirect impacts on tick abundance. Due to the complex nature of the tick life cycles' that occur both on and off-host, these studies are unlikely to fully capture real-world tick population abundance changes in which wild ungulate herbivores and livestock are present on the landscape under changing climatic conditions.

Developing a better understanding of the role of climatic conditions in modulating herbivore effects on tick abundances will be increasingly important (**Sources Needed**). Another vital facet to this is the addition domestic herbivores on landscapes. Our study addresses this knowledge gap by investigating direct vs. indirect effects of changes in herbivore assemblages—livestock additions and wildlife declines—across varying climate conditions. We used a series of experimental large herbivore exclosures replicated across a topoclimate gradient to quantify the interactive effects of large wild ungulate removal, livestock addition, and climatic context on small vertebrate host abundance and tick density. Data collection on tick and host abundances occurred prior and after experimental manipulation and encompassed an entire generation of the three-stage hard-bodied tick populations present on the landscape.

This study took place at the Tejon Ranch Exclosure Experiment (TREE), in an oak savannah system in southcentral California, US, and is the first study of its kind in the region. California's oak savannas are experiencing rapid dual changes in climate and ungulate assemblages and have been the focus of detailed experiments and climate change forecasting (**Sources Needed**). TREE utilizes a replicated system of three exclosure types to alter herbivory pressure of cattle and wild

ungulates across three disparate climate zones. Data collection addresses three questions for this system. 1) How does large mammal modification impact tick abundance? 2) How do changes in large herbivore assemblages' impact small tick host (lizard and mammal) abundance and diversity? 3) How does climate mediate the impacts of the prior questions? We hypothesized: i) Large herbivore removal will have a strong effect on tick abundances ii) small-mammal hosts will increase in abundance when large mammals are excluded, and (iii) the strength of these effects are contingent on climatic context and are strongest in more arid, low-productivity areas.

MATERIALS AND METHODS

Study area:

We conducted this study within TREE in Kern Co., CA (34°59'N, 118°43'W). Tejon is a mixed cattle-ranch and wildlife conservation property, containing 97,124 hectares of conserved lands. 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 at an average stocking density of 0.13 head/ha (personal communication). All plots were established in mixed oak savanna-woodland composed of blue oak (*Quercus douglasii*), valley oak (*Quercus lobata*), California black oak (*Quercus kelloggii*), and occasionally Ponderosa pine (*Pinus ponderosa*). Plots spanned an elevation range from 580-1650 m. Understory was dominated by exotic annual grasses, annual forbs, and woody shrubs (*Erica*, *Ribes*) at higher elevations (above ~1220 m).

Experimental design:

The TREE is an ongoing study consisting of 27 1ha plots, initiated in 2016 to understand the ecological effects of shifting wildlife and livestock assemblages across varying climates (Orr et al., in revision). The 27 experimental plots spanned three aridity levels, and each level included three replicate randomized blocks. Each block contained three treatment levels of large herbivores – a) *no wild ungulates or livestock* (total enclosure) which functionally excluded all large herbivores over 40 kg body mass with complete barriers of barbed wire fencing, b) *wild ungulates only* (partial enclosure) which used semi-permeable fencing to remove livestock, and c) *both wildlife + livestock* (open) which has no fencing and demarcated plot corners with t-posts. Monitoring of dung counts across all plots confirmed that treatments operated as intended (Fig X). Intensive monitoring and incorporation of temporal and spatial variability in these replicate experimental plots, as well as use of a replicated before-after-control-impact design. These experimental designs were targeted to help control for the inherent challenges of sampling ticks in the far-western United States where there is a high degree spatial and temporal variability in both questing ticks, vertebrate populations, and vertebrate tick burdens.

[HERBIVORE ABUNDANCE FIGURE HERE?]/ [Map & plot schematic here]

Climate data:

The study area is characterized by rugged topography creating steep aridity gradients, providing strong local variation in climate (temperature, relative humidity) 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. Monthly maximum and minimum temperature data as well as monthly precipitation data was collected from regional NOAA weather stations (cite). The weather stations were selected on their similarity in elevation to the study sites, their coverage of the data, as well as their latitude and longitudinal closeness to the field site locations.

Questing ticks

The effect of large herbivore removals on the density of questing ticks was evaluated by sampling questing ticks in the year of the experiment initiation (2016) and the first three years of the experiment (2017-2019). Each plot was sampled for ticks by dragging a 1 m² white flannel cloth through the understory. Each plot was sampled twice a month for 1 hour during the peak questing period for *Ixodes pacificus* (vector of Lyme disease) from April to June. During other times of year, plots were dragged for 1 hour once a month. All ticks present on the cloth were collected with tweezers and stored in 70% Ethanol. Ticks were identified by species in the field, and if further confirmation was needed, they were taken back to the lab for further examination under a light microscope.

Small Vertebrate Hosts

Lizard visual mark-recapture surveys:

Western fence lizard populations were surveyed using a mark recapture approach at all plots in late spring-summer, the peak season of juvenile tick questing in this region. At each plot, we visually surveyed lizards along six evenly spaced transect lines, 10 m apart. Sighted lizards were sprayed on their dorsum with a diluted latex paint mixture using an Idico hand tree-marking gun (Idico Products Co., Miami, FL, USA, cite), enabling the marking of lizards from 5 to 10 m away (e.g. without handling them). This marking was temporary, lasting only until the lizard's next molt (cite- Dr. Swei lizard removal paper 2011). We surveyed lizards in each plot on three consecutive days between 10 am and 4 pm in warm weather with limited wind or cloud cover, using a different paint color each day to determine a lizard's encounter history.

Small mammal density and burden:

We sampled small mammal populations annually at all plots (summer 2016, fall 2017, fall 2018)). Trapping in the fall and spring in 2019 focused efforts on one block in Mesic and one block in Arid, where past trapping efforts had yielded the greatest number of mammals. Small mammals were trapped using extra-large Sherman live traps (7.62 9.53 30.48 cm; H.B. Sherman Traps, Tallahassee, FL, USA) for three consecutive nights. Each plot was arrayed with 5 rows of 10 trapping stations. Each row was 10 m apart for a total of 50 traps per plot per night (for a total of 50 traps*3 nights*27 trapping events =4,050 trap hours). All captured animals were given an individually numbered fingerling eartag (National Band and Tag Co., Newport, KY, USA), identified by species and sex, and weighed before being release on site. All ticks were removed from the ears and head of each animal before being released at the point of capture.

Data analyses:

Data characteristics

The outcome of interest for most statistical analyses focused on questing tick counts that were collected almost monthly from 2016 through 2019. Since abundance of *I. pacificus* was low, tick

totals of all species (*I. pacificus*, *D. occidentalis*, *D. variabilis*) were combined in the analysis. All analyses were performed in R (v 1.3.1093).

Tick density relationships with cattle and climate

For our outcome of interest - tick counts - we fitted generalized linear mixed models (GLMMs) with a negative binomial regression to calculate an extra parameter for overdispersion (Richards 2008). To test the effects of two environmental stressors - cattle and climate - on tick counts we fit a GLMM with fixed effects a) cattle grazing treatment, b) climate aridity level and c) their interaction as well as random effects plot ID and month. All models were constructed using the function ``glmer.nb`` in the ``lme4`` package (Bates et al 2015).

Vertebrate abundance and diversity estimates

To quantify the impacts of cattle and climate on lizard and mammal population estimates we used a Wilcoxon rank-sum test. Vertebrate populations abundances were estimated for each experimental plot when sampling of three consecutive days occurred with the ``Rcapture`` package (Baillargeon and Rivest 2007). Both lizard and rodent Shannon diversity indices were calculated using the ``vegan`` package (cite).

Tick density and vertebrate population estimates

To measure the experimental design impacts on vertebrate populations and indirectly on ticks, we correlated counts and vertebrate population estimates we conducted a Spearman's rank correlation test between tick counts and a) lizard or b) mammal population estimates with ``cor.test`` function.

Model comparisons

Model comparison was used for each model structure type and the best fit model was selected based on the following criteria: the lowest value for Akaike's Information Criterion (AIC), adjusted R^2 , and rules of parsimony. Additionally, to get relative support for each model we standardized the likelihood of the models to get the Akaike weight.

RESULTS:

Tick abundances

Sampling from 2016 – 2019 resulted in 2,692 questing ticks. The most common tick species collected via tick drag were *Dermacentor occidentalis* (n = 2,420, 89.9% of the collected tick population), *Ixodes pacificus* (n = 206, 7.7%), and *Dermacentor variabilis* (n = 68, 2.5%) (Supplemental Table). Efforts to collect the juvenile life stages of both tick species proved difficult and therefore only the adult life stages were included in the analysis. Total tick abundance varied seasonally (62%, or 1,671 of the total ticks were collected in April and May) (Fig of month), and the scale and timing of fluctuations differed among tick species (Supplemental Table). Tick counts as a response to cattle grazing pressure (plot) were significant for Total and Partial plots (Fig coefficients, Supplemental Fig table) with triple the tick count in Total (n = 1,228) compared to Open (n = 488) plots. Tick counts as a response to climate aridity levels (site) were significant for Intermediate and Mesic sites (Fig coefficients, Supplemental Fig table) with Intermediate having the most tick counts (n = 1,764). Questing tick counts were

greatest in 2017 (n = 1121), one year post fence set up, followed by 2018 (n = 785) and 2019 (n = 733) (Supplemental Fig).

How do environmental stressors – cattle and climate – impact tick counts?

Tick counts were best explained by the GLMM that included both fixed effects cattle and climate with plot ID and month as random effects. If each stressor, cattle and climate, were evaluated independently for their effect on tick counts, climate would be the stronger predictor (Fig coefficients, Supplemental Fig table). However, models that incorporated both cattle and climate performed better than single predictors. Models that included cattle and climate interaction term failed to converge. If individual random effects were considered with the fixed effects cattle and climate, the model that included only month (AIC = 3837.2) was a better fit than the random effect block (AIC = 4278.2). However, the best fitting model included cattle and climate as fixed effects and block and month as random effects (AIC = 3764.9, Pseudo-R² (total) = 0.81, p-value = 0.000187) (Fig coefficients, Supplemental Fig table).

How do environmental stressors impact population estimates of lizards and mammals, two important vertebrates in the tick system?

Each vertebrate group was impacted differently by the experimental setup (plot or site) with lizard population estimates responding more strongly to climate aridity levels (site) whereas mammals responding more to cattle grazing pressure (plot) (Supplemental Fig). Based on sampling sessions across the entire study, lizard population estimates (n = 1,799) were three times higher than mammal population estimates (n = 561). Despite the smaller sample size (Supplemental Fig), mammal population estimates trend higher in enclosure plots Total (n = 196) and Partial (n = 305) compared to Open (n = 61) plots. Whereas lizard population estimates were significantly different by site type (Wilcoxon rank sum: W = 11, p-value = 0.01306) and non-significantly different by plot type. The median of lizard population estimates by site types were doubled in Intermediate (n = 134) compared to Arid (n = 70). Shannon diversity indices of mammal populations increased with enclosure intensity (Open = 0.60675, Partial = 0.89183, Total = 0.9269) but was not statistically significant.

Are vertebrate population estimates correlated with tick counts?

We found that lizard population estimates were significantly and positively correlated with tick counts (p-value = 1.76e-05, rho = 0.17) whereas mammal population estimates were not significant or correlated (p-value = 0.37, rho = -0.04).

DISCUSSION:

Our study explored the effects of two environmental stressors – cattle and climate – on tick and small vertebrate host abundances across a topoclimate gradient using a replicated enclosure experiment for multiple years. We found that both stressors impact tick counts and can potentially be explained by direct (physical changes to the ecosystem) or indirect (changes to tick-host interactions) effects. Tick abundances varied by tick species, temporal scales (months within a year, or across 3 years) and experimental design (as a response to climate aridity levels or cattle enclosure). The total number of questing ticks was significantly greater within Partial and Total enclosures than in Open (unfenced) control plots and increased with each successive level of large-herbivore removal. This effect was strongest under intermediate climatic

conditions, indicating that climatic context and wildlife removal can interact to affect tick abundance.

Ticks rely on blood meals from small vertebrate hosts to complete their life cycle. Large herbivores are known to alter small mammal communities which can then have indirect impacts on tick populations. While small mammal population estimates were higher in the Partial and Total exclosures when compared to the Open plots, the increase in population estimates was marginally non-significant. This result could be due to low sample size despite trapping efforts or a time lag of when fences were first established at exclosure plots. Questing adult tick populations were the greatest in 2017 (one year post fence implementation) and slowly declined until 2019. Whether this trend represented an effect of the fences on vertebrate hosts and then tick populations or coincidence is difficult to disentangle but may be more feasible to answer with additional years of sampling. Still the increase in tick populations in each successive level of herbivore removal is not enough to solely explain exclosure tick abundance. Previous studies have interpreted tick increases following large herbivore removal as being driven by increases in smaller mammalian hosts in the absence of megafauna and have concluded by suggesting that prevention of wildlife loss might help prevent an escalation in the number of questing ticks infected with zoonotic pathogens (Titcomb et al. 2017). However, both the absence of a significant increase in small mammals coupled with immediate increase in tick abundances suggests alternative mechanisms at play.

An alternative mechanism has been suggested by Esser *et al.* (cite) and Buck & Perkins (cite), namely that tick increases might be an artefact of our experimental plot sizes (each 1 ha), and that in the absence of final hosts, ticks might have dispersed into the exclosure plots via rodent hosts. If this is the case, then the observed pattern is scale-dependent, and ticks might not proliferate following large-scale large-mammal extirpation scenarios because final hosts are entirely lost. Such scale-dependence has been observed in North American deer exclosures (**Sources Needed**). While rodents could import immature ticks across plot boundaries (an effect that would probably most pronounced at plot edges), to fully explain our results this would require very large numbers of plot-crossing rodents and/or very high densities of ticks per rodent (which is not common in the US far west tick system compared to the northeast system). We observed neither in our small mammal trapping, suggesting low likelihood of this scenario in our system, especially in Arid and Intermediate sites, where the rodent population at times drops to near zero.

A narrative to the tick proliferation we consider more likely is that the hares, sciurids, and small carnivores present in the exclosures sustain tick populations by hosting gravid females that can produce thousands of larvae that quickly attach to abundant intermediate hosts (**Sources Needed**). In this system--and indeed, most systems--the complete extirpation of all possible hosts is not feasible. This is especially the case for *D. occidentalis*, which exhibits a high degree of host generalism in small and medium sized mammal species (Eisen et al. 2006, Padgett et al. 2016, Slowik and Lane 2009). Therefore, even if the patterns we observe are due to “pooling” of ticks that are transported into exclosure and then unable to attach to hosts, this increase is still relevant to understanding tick population proliferation on the landscape.

Another mechanism likely related to tick population success in the exclosures is the improvement of environmental conditions. Increased vegetation density from decreased grazing pressure may lead to an increase in preferential habitat areas for ticks (**Sources Needed**). Increased plant biomass lowers soil and above ground temperatures, which are beneficial to tick questing activity, particularly for the more environmentally sensitive immature stages (**Sources Needed**). Because larval mortality is usually very high any improvements in environmental conditions can increase contact rate with intermediate hosts in the absence of megafauna [**cite; Orr et al. in revision; Orr et al. in prep**] and may substantially elevate larval survival and in turn the abundance of questing adults.

An entire investigation into tick abundance and density at all life stages (larval, nymph, adult) was not completed by this study due to the very low collection numbers of larvae and nymphs in the control and exclosure plots via the dragging method for collection. This has been the case with other studies in southern California and a function of a warmer, drier climate that reduces the amount of time juvenile ticks are able to quest above ground (**cite Lane, Padgett papers**). In addition, the capture of medium sized mammals did not occur in this study. An aim for future work would include the collection of immature stages either through a method in addition to dragging and additional captures of some of the prominent medium sized species on the landscape.

In addition to large herbivore exclusion, climate - mediated by topographic change was a significant variable in tick abundance and in modeling tick counts. Climate in conjunction with herbivore presence presented the greatest extremes in limiting tick abundance in the Open controls at Arid. Climate and herbivore removal mediated the highest instances of tick abundance at the Intermediate exclosure. Although models that incorporated both cattle and climate produced the strongest models, if stressors were evaluated independently, climate was a stronger predictor for tick counts than cattle (Fig coefficients, Supplemental Table).

Ticks are a Holarctic species and generally prefer mild to moderate temperatures (0-33 degrees C) (**Sources Needed**). In California, *I. pacificus* has a maximum temperature range of 23-33 degrees C (Eisen et al.), and prolonged temperatures 32-40C can decrease survivorship and reproductive success (Eisen et al. 2018). The heat especially during the summer months likely causes quicker desiccation-related mortality. High tick abundance at the Intermediate climate likely resulted from its cooler temperatures than arid, but lower temperature variability than Mesic (Fig). Additionally, the existence of a mid-level shrub (primarily rabbit brush) layer at intermediate may have contributed increased shading and relative humidity relative to arid (Orr et al in prep). The arid climate has no shrub understory, only a grassland dominated groundcover. Other studies of tick populations in California have noted that grassland ecosystems are less conducive to tick populations than other more moisture conserving habitats (**MacDonald et al...Eisen...others**) The lack of shrub cover, combined with the high temperatures, may potentially put ticks at greater risk of desiccation and contribute to either lower abundance and/or extremely truncated questing activity (Fig).

Climate had a significant effect on lizard populations (Fig), whereas exclosure treatment did not. Like ticks, the current lizard populations may be reliant on a climatic zone that has adequate precipitation and a preferably temperature range, particularly for these ectothermic animals.

Their population numbers at this climate may be the same as those that permit for the greatest tick abundances (**Sources Needed**). The importance of lizard population estimates suggests a possible population rebound for these species is occurring after the intensive drought period that occurred in California between 2011 and 2017 that was particularly extreme in Southern California (**Sources Needed**). While not a primary host for *D. occidentalis*, lizards (*S. occidentalis*) are a primary host for *I. pacificus* (**Sources Needed**), the species with the second highest tick abundance in our study. The resurgence of these populations may have implications for an increasing abundance of *I. pacificus* (**Sources Needed**). Although lizards are not a reservoir for *B. burgdorferi* (agent of Lyme Disease), increasing the *I. pacificus* abundance would likely increase *B. burgdorferi* (**Sources Needed**). A continual recovery of lizard populations in similar habitats to Intermediate throughout Southern California could hold implications to future Lyme disease prevalence in this geographic area.

A limited amount of tick-borne disease research has occurred in southern California despite its well-suited natural design to understand the impacts of climate and land use on tick populations. Tick populations are present in southern California and can reach comparable densities to northern California along coastal communities (**Salkeld, Sambado in prep**). These southern tick populations present a unique opportunity to test the many mechanisms that shape tick dynamics in addition to natural phenomenon like drought and fire which are occurring at an increased rate and scale in California and throughout ticks North American range (**MacDonald, etc**). While we have significant trends in our tick abundance data across climate and cattle stressors, ticks and vertebrates (lizards, mammals, herbivores) may have not yet recovered from the 2011-2017 drought which could put additional stress in the tick system as species compete for resources.

Our study highlights the challenge of predicting the effects of either biodiversity loss or climate change in isolation of other stressors on vector ecologies and infectious disease dynamics. Tick borne diseases are on the rise globally, their ranges will be in fluctuation with ecosystem changes brought about by climate change so their monitoring into the future is important. Furthermore, the costs of wildlife loss on tick-borne disease in this region may be intensified in drier, less productive areas that are likely to worsen with a changing climate (**Sources Needed**).

Conclusions (needs re-write):

Our study demonstrates the significant potential for shifting large herbivore assemblages to alter the risk of tick populations. Our results suggest consistent context-dependent patterns, indicating that despite the inherent complexity of tick life cycles, responses to large herbivore additions and losses are remarkably quick and predictable under certain environmental conditions.

FIGURES

Main text

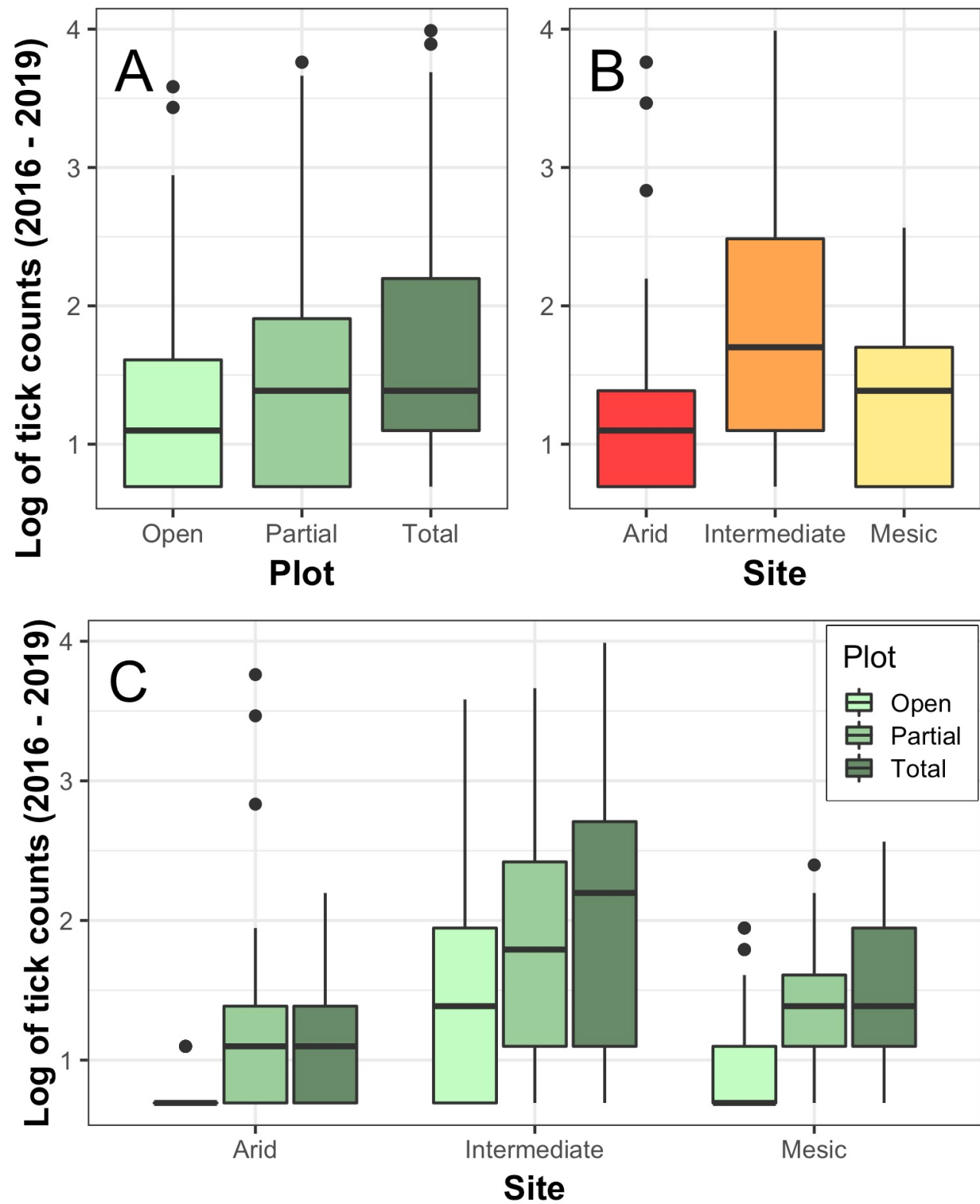


Figure 1.

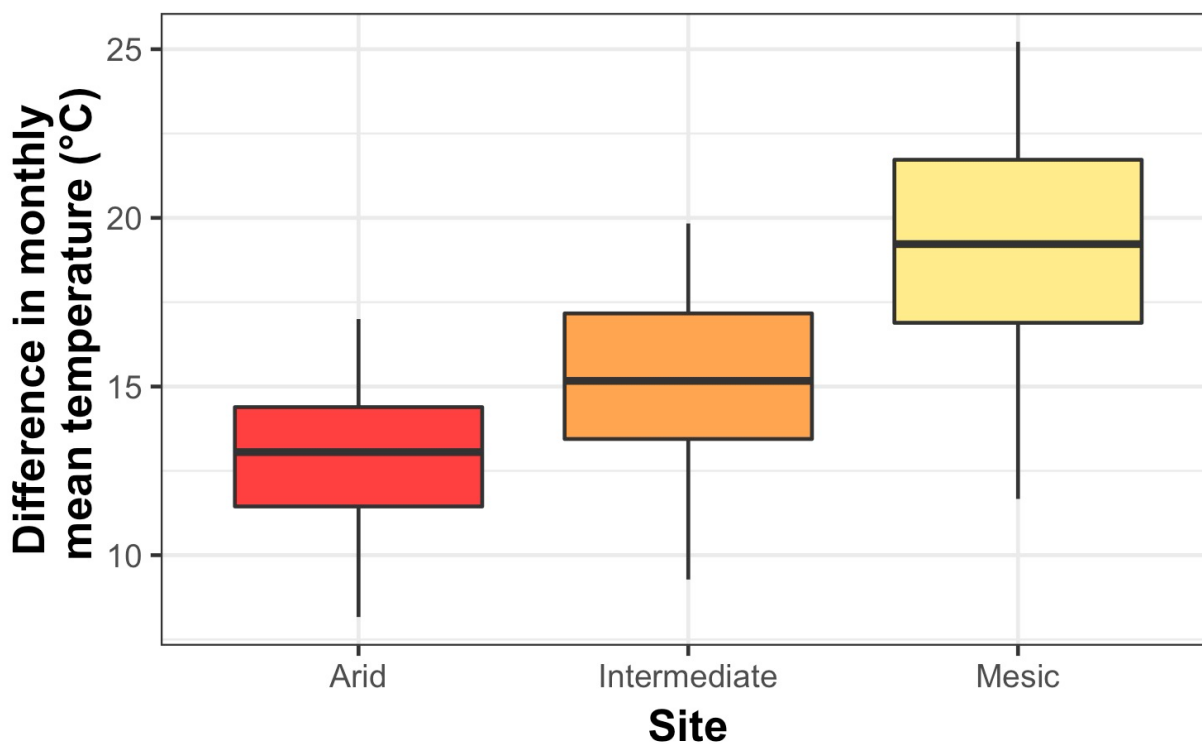


Figure 2.

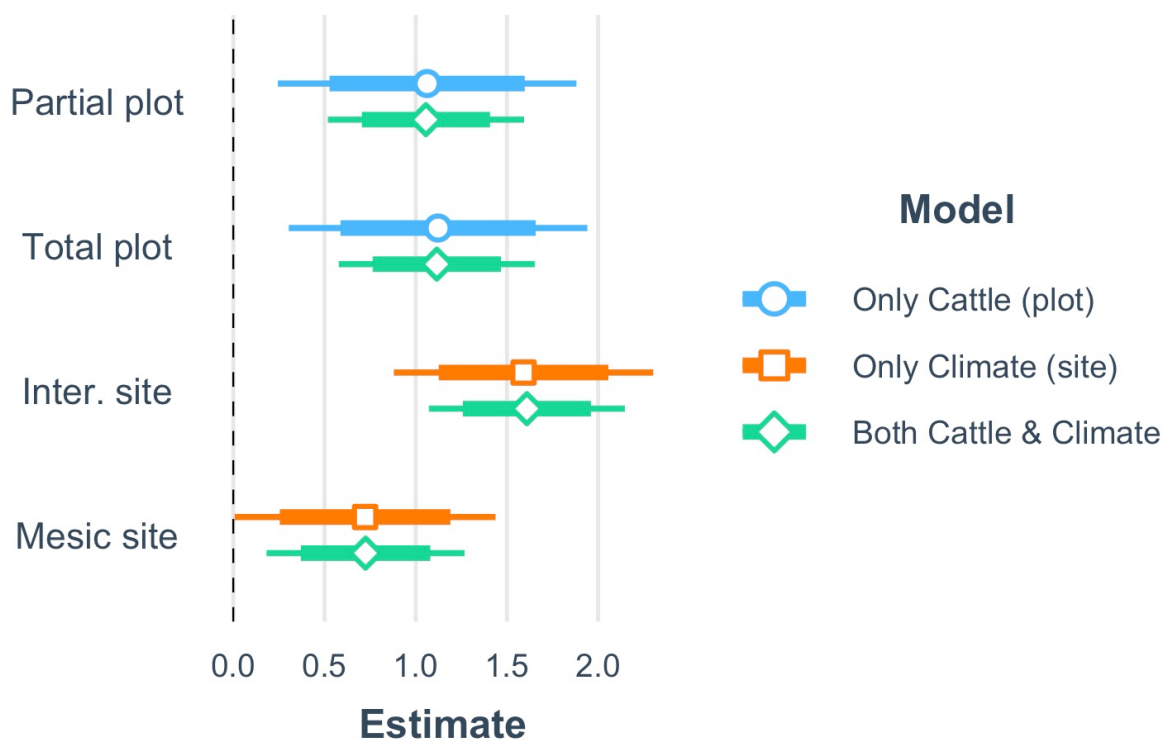


Figure 3. GLMM negative binomial model estimates.

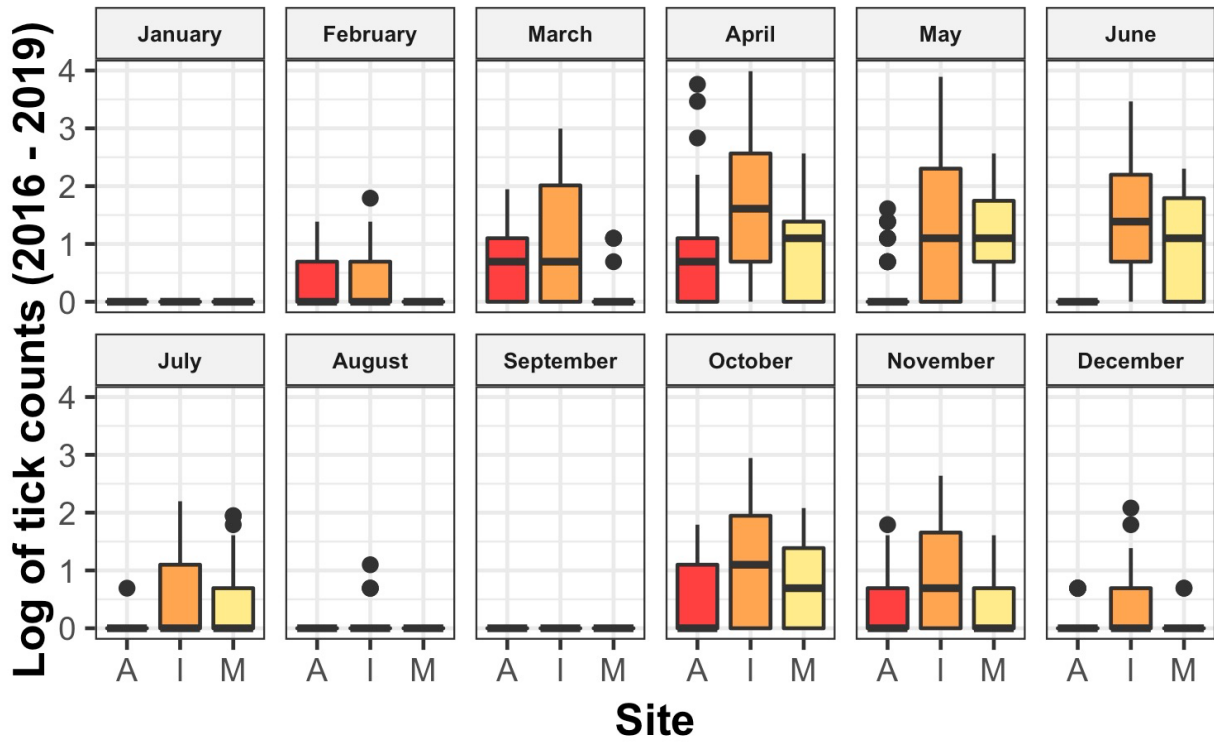


Figure 4.

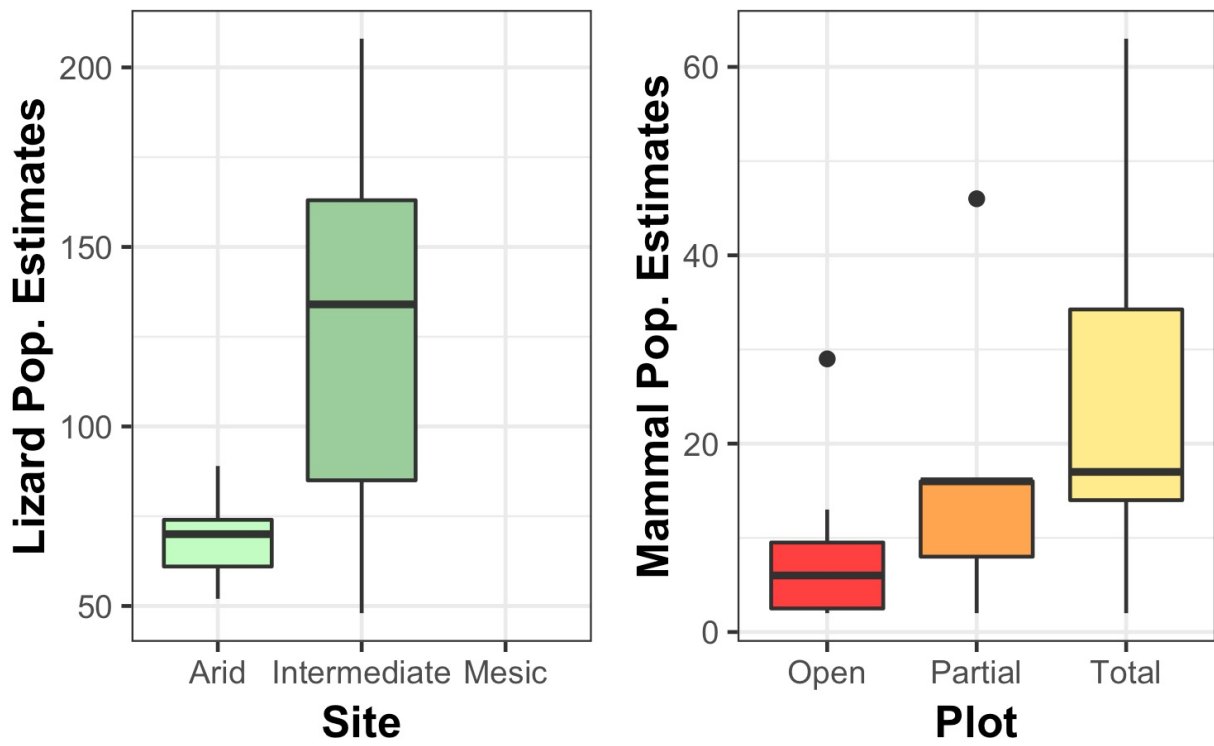


Figure 5.

Supplemental

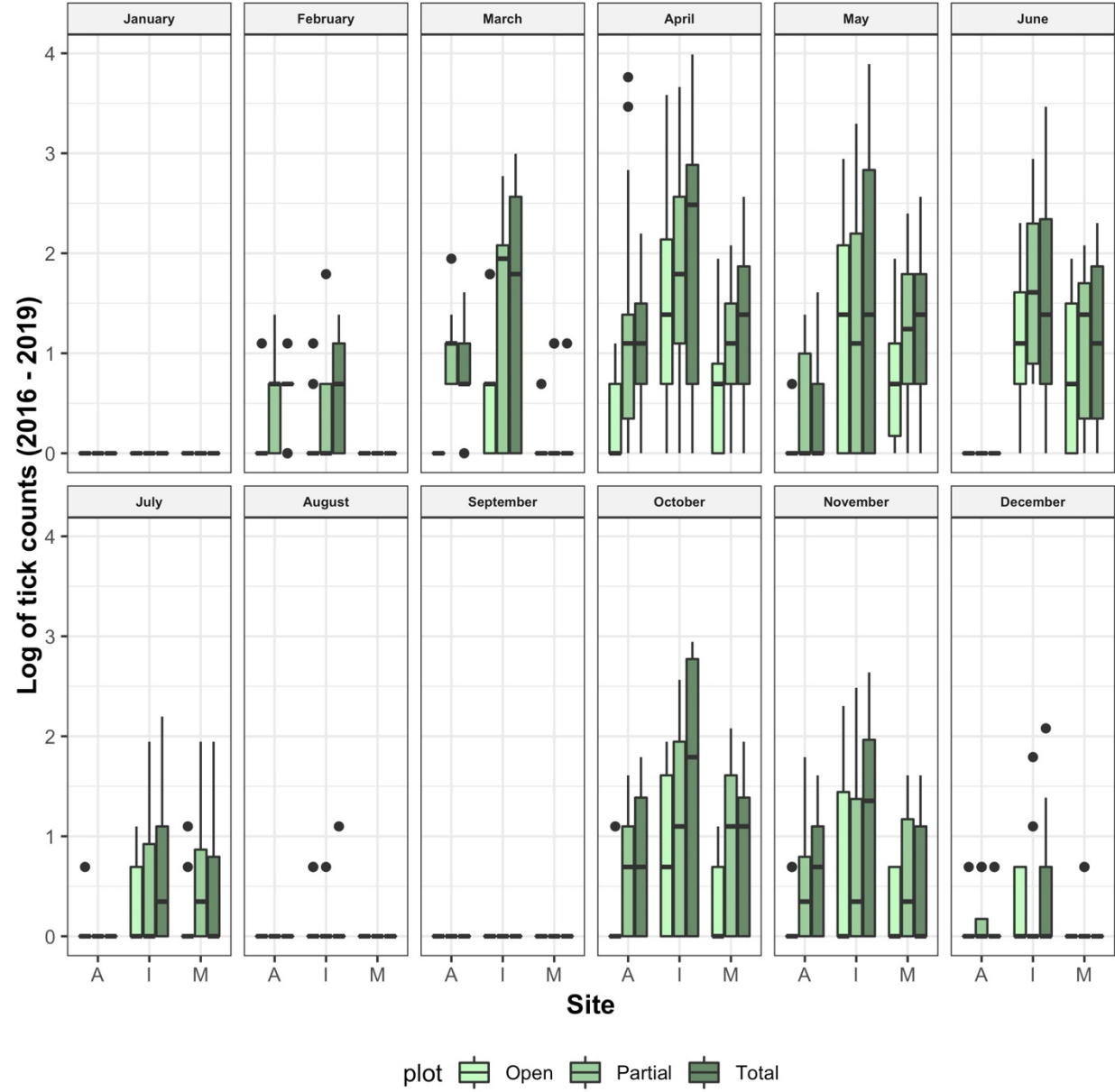


Figure 6.

	Model 1	Model 2	Model 3
(Intercept)	-2.05 ** -2.69, 95.00% CI [-3.53, -0.56]	-2.08 ** -2.80, 95.00% CI [-3.54, -0.62]	-2.82 *** -3.78, 95.00% CI [-4.28, -1.36]
plotPartial	1.06 * 2.54, 95.00% CI [0.24, 1.88]		1.06 *** 3.85, 95.00% CI [0.52, 1.59]
plotTotal	1.12 ** 2.69, 95.00% CI [0.30, 1.94]		1.12 *** 4.06, 95.00% CI [0.58, 1.65]
siteIntermediate		1.59 *** 4.38, 95.00% CI [0.88, 2.30]	1.61 *** 5.87, 95.00% CI [1.07, 2.15]
siteMesic		0.72 * 1.98, 95.00% CI [0.01, 1.44]	0.72 ** 2.62, 95.00% CI [0.18, 1.27]
N	1395	1395	1395
N (plotID)	27	27	27
N (month)	12	12	12
AIC	3783.46	3776.80	3764.85
BIC	3814.91	3808.24	3806.78
R2 (fixed)	0.03	0.05	0.09
R2 (total)	0.81	0.81	0.81

All continuous predictors are mean-centered and scaled by 1 standard deviation. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Table 1. GLMM negative binomial output. Model 1 = counts ~ cattle + (1 | month) + (1 | plotID). Model 2 = counts ~ climate + (1 | month) + (1 | plotID). Model 3 = counts ~ cattle + climate + (1 | month) + (1 | plotID)

Model Selection								
tick count ~ plot + site + plot*site								
(Intercept)	plot	site	plot:site	df	logLik	AICc	delta	weight
-1.966113	+	+	+	9	-4,002.64	8,023.40	0.00	1.00
-0.889414	+	+	NA	5	-4,052.37	8,114.79	91.39	0.00
-0.280302	NA	+	NA	3	-4,222.39	8,450.79	427.39	0.00
0.048278	+	NA	NA	3	-4,628.59	9,263.20	1,239.80	0.00
0.657390	NA	NA	NA	1	-4,798.61	9,599.21	1,575.81	0.00

Table 2. Model selection with Akaike weight.

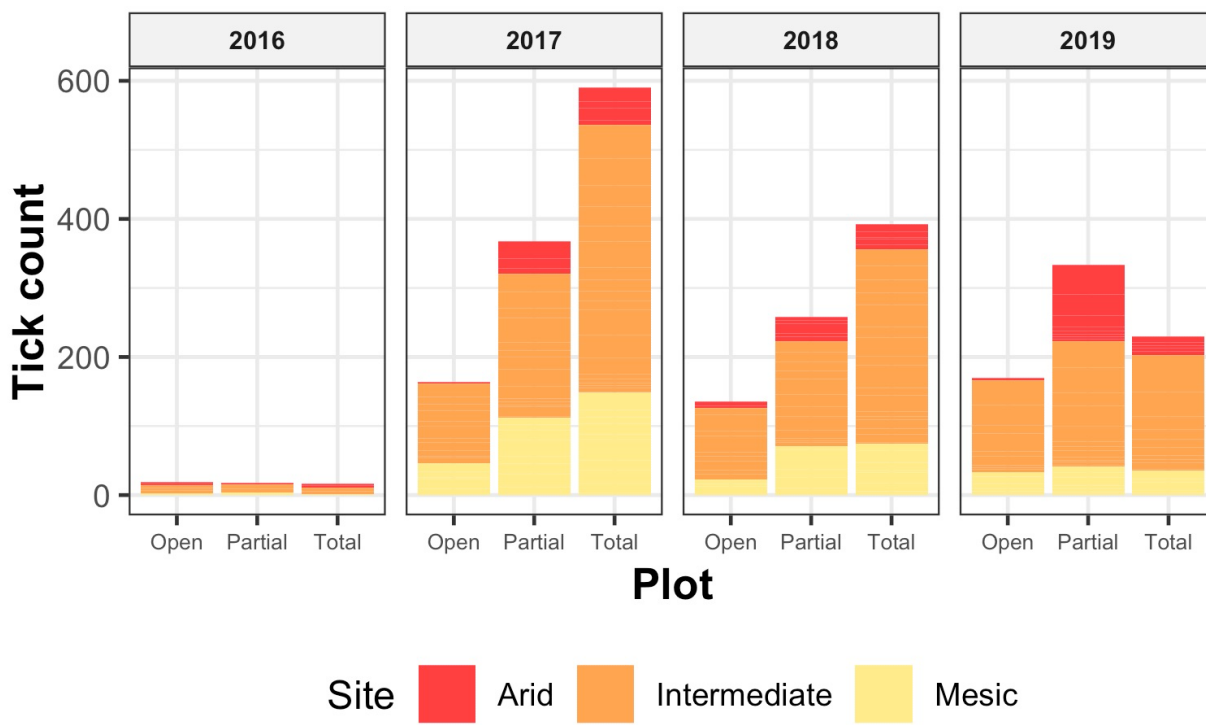


Figure 7.

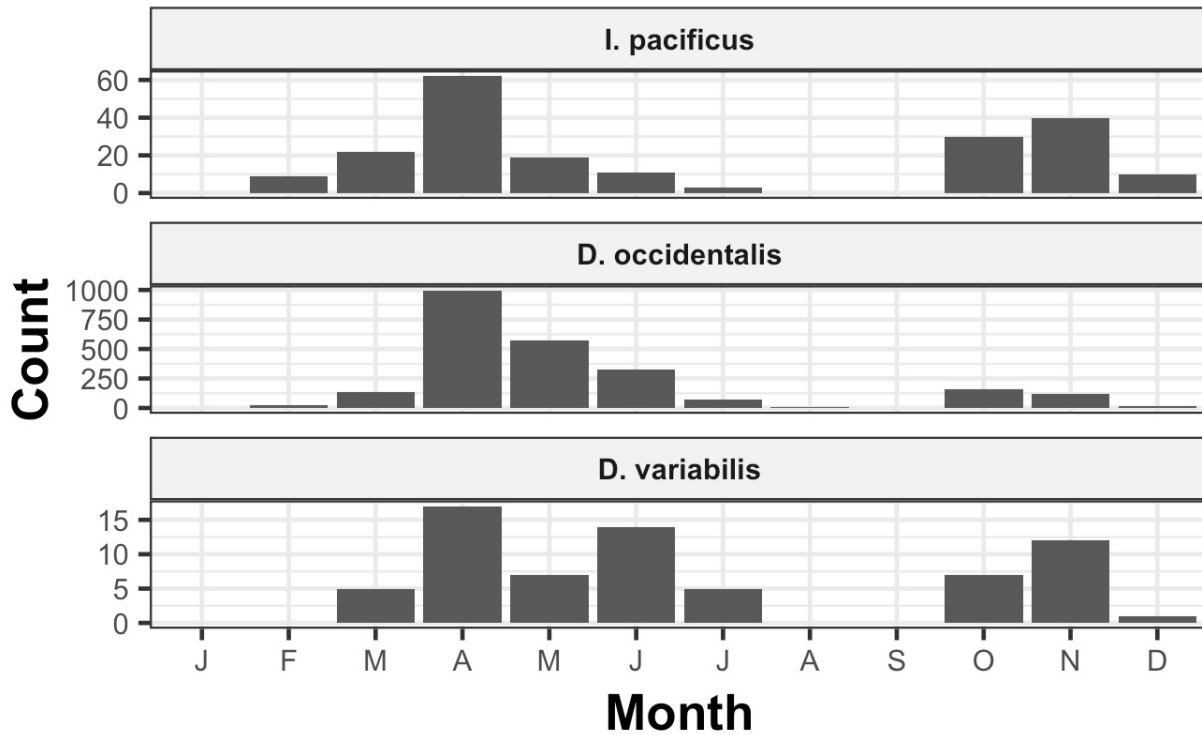


Figure 8.

site	plot	n
Arid	Open	21
Arid	Partial	195
Arid	Total	124
Intermediate	Open	364
Intermediate	Partial	554
Intermediate	Total	846
Mesic	Open	103
Mesic	Partial	227
Mesic	Total	258

Table 3.

Month	IPAC	DEOC	DEVA
January	0	0	0
February	9	28	0
March	22	132	5
April	62	990	17
May	19	574	7
June	11	325	14
July	3	71	5
August	0	5	0
September	0	0	0
October	30	159	7
November	40	116	12
December	10	20	1

Table 4.

Site	Plot	PEMA	PEBO	PECA	PEXX	CHCA	NEMA	Other	Total
Arid	Open	7	1	0	0	0	0	5	13
Arid	Partial	23	10	0	1	2	0	6	42
Arid	Total	12	12	0	4	1	0	5	34
Intermediate	Open	7	1	0	0	0	0	0	8
Intermediate	Partial	9	3	0	0	0	0	0	12
Intermediate	Total	17	6	0	0	0	0	0	23
Mesic	Open	17	9	14	0	0	0	8	48
Mesic	Partial	19	8	17	0	0	3	15	62
Mesic	Total	17	12	31	1	0	0	11	72

Table 5.