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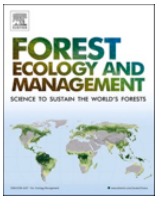

Interactive effects of large herbivores and climate on California oak seedling outcomes

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A B S T R A C T

The perpetuation of tree populations is dependent on successful seedling establishment, which is in turn controlled by biotic and climatic factors. California's endemic oak species face limited recruitment and shrinking ranges due to anthropogenic climate change and land use, both of which can negatively impact germination and seedling survival. In this study, we investigated *Quercus* seed germination and seedling establishment under three large herbivore regimes (no large herbivores, wild herbivores, and both wild herbivores and cattle) across three sites representing present, near-future, and far-future projections for climate in California's montane oak woodlands. Seed germination and living seedling abundance were highest in the intermediate and mesic climate levels, where total exclosures resulted in the best outcomes for seedlings. In contrast, in the arid level, the best large herbivore regime for establishment consisted of wild herbivores and no cattle. Seedling mortality was highest in the most arid climate level, and within that level, mortality was reduced by over 25% in both the wildlife and wildlife plus cattle treatments compared to the total exclosures. Our results suggest that increasing aridity will limit oak establishment and modulate the impact of large herbivores on oak seedlings, with wild large herbivores becoming a beneficial factor for seedling abundance, and both wild herbivores and cattle reducing mortality. Dynamic and contextually informed management of large herbivore populations and other restoration actions will be necessary to ensure the sustainability of California's oak populations.

1. Introduction

Climate and herbivory are two major drivers of change in forest ecosystems, and the interaction of these two factors will determine the future trajectory of tree populations (Fisichelli et al., 2012; Post and Pedersen, 2008). One pathway by which climate and herbivory alter forests is via seedling establishment, which is highly sensitive to both biotic and abiotic controls (Frei et al., 2018; Grubb, 1977; Harper, 1977). The seedling stage is a high-mortality life stage that can limit tree recruitment and govern species range shifts (Boerner c Brinkman, 1996; Jackson et al., 2009; Middleton et al., 1991; Zhu et al., 2012). Anthropogenic changes in land use and climate, therefore, may add obstacles to the already precarious process of seedling establishment, the first step to sufficient recruitment.

Large-scale land conversion and climate change threaten the existence of oak woodlands and savannas in the California Floristic Province, a global biodiversity hotspot (Byrd et al., 2015; California Department of Forestry and Fire Protection, 2018; Allen-Diaz et al., 2007; Myers et al., 2000). Endemic tree species such as valley oak (*Quercus lobata*), blue oak (*Q. douglasii*) and California black oak (*Q. kelloggii*) compose much of California's oak woodland habitat (Davis et al., 2016a), where *Quercus* is among the most important genera used by wildlife for food and cover (Little et al., 2001; Tietje et al., 2005; Verner, 1980). These oak species employ a masting strategy wherein they periodically produce large quantities of acorns (Koenig et al., 1994), and the high-mortality seedling stage is considered a demographic bottleneck in the maturation of these acorns into adult oaks (Tyler et al., 2002). Unfortunately, millions of acres of oak-dominated systems in the state have been lost to land conversion for irrigated pastures, agriculture, and urban development (Bolsinger, 1988; Sleeter et al., 2011). Endemic species such as California's endemic oaks face even greater risks from human activities because of their limited geographic distribution (Dobrowski et al., 2011; Forero-Medina et al., 2011; Loarie et al., 2008). These anthropogenic factors, combined with naturally low rates of recruitment and highly variable yearly seed production (Koenig and Knops, 2013), have resulted in an uncertain future for oak populations in California (Tyler et al., 2006).

One of the key factors limiting recruitment in California's oak

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populations are ungulate herbivores, which can impact seedling establishment through both direct and indirect mechanisms (Davis et al., 2019; Tyler et al., 2006). The oak seedling stage is especially sensitive to biotic and abiotic influences of large ungulates (Barrere et al., 2021; García and Houle, 2005; Gribko et al., 2002), but oaks may also derive less benefit from the exclusion of herbivores than other tree species (Laurent et al., 2017). Large herbivores typically exert a negative influence on seedling survival, primarily through direct browsing damage (López-Sánchez et al., 2014; Swiecki et al., 1997), but also through a reduction of water availability by promoting invasive grasses (Danielsen and Halvorson, 1991; Gordon et al., 1989). In other circumstances, however, cattle and wild herbivores may benefit seedling survival by reducing interference from other plants or eliminating habitat for rodent herbivores of seedlings (Adams et al., 1991; Bernhardt and Swiecki, 1997; Tyler et al., 2006). Furthermore, both cattle (López-Sánchez et al., 2014; Standiford et al., 1997) and wild large herbivores (Callaway and D'Antonio, 1991) have been suggested as a factor in reducing oak seedling density and in shifting oak species composition by preferentially browsing deciduous species, including valley, black, and blue oak, rather than evergreen oaks (López-Sánchez et al., 2019; Perea et al., 2017). While available data suggest that there is no difference between the effects of wild large herbivores and cattle on oak recruitment (Hall et al., 1992), no studies have investigated the varying effects of different herbivores using simultaneous experimental manipulation of both cattle and wildlife. Across California, wild large herbivore populations face varying trajectories: populations are increasing due to successful reintroductions in some areas, and declining due to habitat loss, predation, and hunting in others (California Department of Fish and Wildlife, 2018; California Department of Forestry and Fire Protection, 2018; Casady, 2020; Johnson and Cushman, 2007; Updike and Waithman, 1996; Neal et al., 1987). Cattle, meanwhile, have been widespread across California for hundreds of years (Burcham 1981), and the area of oak habitat used for rangeland increased by 35 percent from 2012 to 2017 alone (National Agricultural Statistics Service, 2017).

The impacts of shifting large herbivore regimes on oak recruitment in California are compounded by changing climatic conditions across the state. Much of the state is experiencing hotter and drier conditions that further disrupt the recruitment process and may make current oak habitat unsuitable for future persistence (Kueppers et al., 2005; McCullough et al., 2015). Water stress can be negatively correlated with seedling emergence (Tyler et al., 2006), but it does not necessarily reduce survival of seedlings once they establish (López-Sánchez et al., 2019). Based on projections of climatic water deficit (CWD) and summer maximum temperature, the area suitable for blue and valley oak seedling establishment may be reduced by 50–95% by the end of the 21st century (Davis et al., 2016b). Even if oak recruitment is currently sufficient to replace mortality, it is poorly understood how climate change will affect survival to the adult stage in the future (Serra-Diaz et al., 2016). Understanding the interactive effects of large herbivores and climatic context on oak populations will be imperative for sustaining the efficacy of ongoing conservation efforts (Perea et al., 2020; Tyler et al., 2006). Monitoring the effects of herbivores on seedling establishment dynamics along environmental gradients is one approach that can resolve this knowledge gap (Gómez-Aparicio et al., 2008; Michalet et al., 2014; van Mantgem et al., 2006). The effects of large herbivore-mediated microsite on seedlings may be dependent on climatic context (Borchert et al., 1989), but it is largely unknown how changes in moisture and temperature may alter the impacts of herbivores on oak recruitment.

Addressing the questions surrounding the impacts of herbivores on recruitment across climate contexts, and the relative importance of wild and domestic herbivores, is critical to identifying best management practices for foundational oak species. Knowing the extent to which, and the contexts in which, particular groups of large herbivores limit oak recruitment is critical to identifying and justifying potentially expensive management interventions (e.g., removing livestock or building cage protections for seedlings). In this study, we sought to determine how the management of wild and domestic large herbivores may be used to promote oak seedling establishment. We used an existing large herbivore experiment across three sites that vary in climatic conditions in the Tehachapi Mountains of southern California. Situated near the southern extent of these species' ranges, endemic oak populations in this region are especially vulnerable to climate change (Davis et al., 2016b; McCullough et al., 2015). We selected three endemic oak species to compare the establishment of species that share similar life histories and occur in close proximity but have different climatic envelopes and therefore different distributions in California. Blue oak is found in warmer, dry foothills, while California black oak prefers cooler and more mesic montane areas (Davis et al., 2016b), and valley oak spans intermediate sites between the two and overlaps with both.

We examined how oak seedling outcomes differed between areas exposed to three large herbivore treatments: no herbivores, wild herbivores only, and both cattle and wild herbivores. Furthermore, we investigated how these effects varied across a spatially distributed moisture and temperature gradient, which served as a proxy for projected reduction in water availability under climate change. We asked: 1) How do climate and large herbivores influence seedling germination and mortality, and 2) Is there evidence of browsing damage as a cause of mortality? We hypothesized that abundance and survival of seedlings would be negatively correlated with the number of large herbivore guilds present (i.e., wild herbivores only or wild and domestic herbivores), and that these effects would be correlated with browsing damage and strongest in the areas with the greatest climate water deficit (i.e., lowest moisture and highest temperatures). This research provides evidence that could help promote oak recruitment through a deeper understanding of how oak seedlings respond to large herbivore management practices under changing climatic conditions (Davis et al., 2016b).

2. Materials and methods

2.1. Study site

We conducted this work at Tejon Ranch, a cattle ranch and wildlife conservation property in the Tehachapi Mountains of southern California (34°59′N,118°43′W). The regional climate is Mediterranean. Mean annual precipitation for the period 1896–2010 varied from around 250 mm in the low elevation portions of the ranch to over 500 mm at the highest elevations. Oak ecosystems in this site are composed of blue and valley oaks (both white oaks), and California black oak (a red oak). The understory is dominated by exotic annual brome grasses (*Bromus* spp.), a mixture of native and exotic forbs/legumes, and shrubs (*Ericameria* sp. and *Ribes* sp.) (Orr et al., in press, *Journal of Ecology*).

2.2. Experimental design

The Tejon Ranch Exclosure Experiment (TREE) is an ongoing study initiated in 2016 to investigate climate-mediated effects of wild large herbivores and cattle on plant communities and associated impacts on other taxa and ecosystem processes. Precipitation at the nearest weather station was 259 mm in the year before seedlings were surveyed (July 2017-June 2018), compared to an average of 340 mm in the July-June periods from 2009 to 2021 (Western Regional Climate Center, 2021). The experiment spans three sites, covering a CWD gradient from 200 to 300 mm. For the period 1997–2017, mean annual precipitation was 352 mm, 419 mm, and 430 mm in the arid, intermediate, and mesic climate levels, respectively, and mean daily average temperature ranged from 12.5 °C in the mesic level to 15.8 °C in the arid level (interpolated PRISM climate data from Orr et al., in press, *Journal of Ecology*). Notably, the intermediate and arid sites represent near-term and long-term climate scenarios for mesic sites, suggesting how climate change may alter oak population dynamics in the future (a space-for-time proxy extrapolation, Blois et al., 2013). At each of the three climate levels, there are three experimental blocks, each with three 100 × 100 m treatment plots (Fig. 1). The three treatments consisted of exclosure plots, with no access for any adult large herbivore species; wildlife plots, which excluded cattle but allowed wild large herbivores; and open plots, with access for both cattle and wild herbivores. Blocks are 100–400 m apart.

Common wild herbivore species in this system include mule deer (*Odocoileus hemionus*), introduced Rocky Mountain elk (*Cervus canadensis nelsoni*), and, occasionally, pronghorn (*Antilocapra americana*), and feral pig (*Sus scrofa*). The ranch hosts around 10,000 head of cattle (*Bos taurus*) at an average stocking density of 0.13 head/ha (personal communication with Tejon Ranch Company), though exact stocking rates vary seasonally and annually. Tejon Ranch, therefore, is a suitable model for California's oak savanna/woodlands and similarly managed oak ecosystems such as those found in Spain, the majority of which are privately owned and support both livestock and wild large herbivores (California Department of Forestry and Fire Protection, 2018; Huntsinger and Bartolome, 1992). The exclosures have been shown to effectively exclude target taxa (>95% reduction in dung of targeted species, Orr et al. in revision). Exclusion of livestock has a neutral to slightly negative impact on wild large herbivore activity in a plot (Fig. S1). Activity of wild herbivores and cattle varied somewhat across climate levels (Fig. S2), with highest wildlife activity at mesic sites and highest cattle activity at arid sites.

2.3. *Understory and canopy surveys*

Species cover was surveyed in each plot within 1 × 1 m subplots spaced every 10 m along six 50 m transects (n = 36 per plot). Cover for each species rooted within the subplot was visually estimated, along with total vegetation, litter, and bare ground cover. All surveys were conducted by the same observers and plants were identified to species using the Jepson Manual (Baldwin et al. 2012). See Orr et al. (in press, *Journal of Ecology*) for a full account of the methods used to survey understory vegetation. Oak tree canopy cover was estimated using satellite imagery from Google Earth Pro (2021) following the methods detailed by Agehara (2020).

2.4. *Seedling surveys*

We surveyed seedlings across all plots in late June 2018. In 2017, all oak species present in the study area produced a large quantity of seeds ("masted"); 2018 therefore represented a year in which seed production was not a limiting factor for the germination and survival of seedlings. By late June, annual vegetation across the study area had partially or fully senesced; this enabled us to 1) more easily locate oak seedlings, 2) have confidence that all seeds had had time to germinate, and 3) enabled sufficient time post-germination (approx. 1–4 months) to assess factors influencing survival (e.g., herbivory or desiccation). In each of the 27 experimental plots, we ran three nonoverlapping 50 m × 2 m belt transects, situated to maximize reproductive adult canopy cover, and therefore represent maximum seedling densities within each plot. We 1) counted total seedlings within a transect, 2) identified the status of each seedling as either alive or dead, 3) noted, for each seedling, if there were signs of above-ground herbivory from wildlife or cattle (hereafter referred to as "browsing damage"). Because seedlings were occasionally clustered together (most likely due to caching by seed predators), individual seedlings were counted as unique meristems associated with a single acorn. Seedlings were considered alive if a leaf or multiple leaves were at least partially green, while individuals were considered dead when all leaves were fully desiccated or removed. Browsing damage from wildlife or cattle was determined by the absence of entire or partial leaves and was easily distinguishable from arthropod herbivory due to magnitude of damage to individual leaves.

While we recognize that seedling responses to factors such as light and water stress vary across other oak species (Brose and Rebbeck, 2017; Rebbeck et al., 2011; Seidel 1972), we were unable to reliably identify all seedlings to species (especially those that had experienced significant herbivory). Thus, all analysis is conducted on data pooled across *Quercus* species. Species of other trees were rare (entirely absent at arid plots) and not included in our survey.

2.5. *Data analyses*

To test the effects of herbivore treatment and climate level on 1) total seedling abundance, 2) mortality, 3) remaining living seedling abundance, and 4) prevalence of browsing damage, we fit generalized linear mixed models (GLMMs). For each of the four response variables, we fit a GLMM including herbivore treatment, climate level, and their interaction as fixed effects, and replicate block and transect as random effects nested within climate level. The interaction term for the models of mortality and browsing damage were not included due to model convergence concerns. For mortality, therefore, we fit a GLMM using only the data from the arid climate level in order to better understand the differences between herbivore treatments in that climate.

To test for differences in canopy and understory structure between

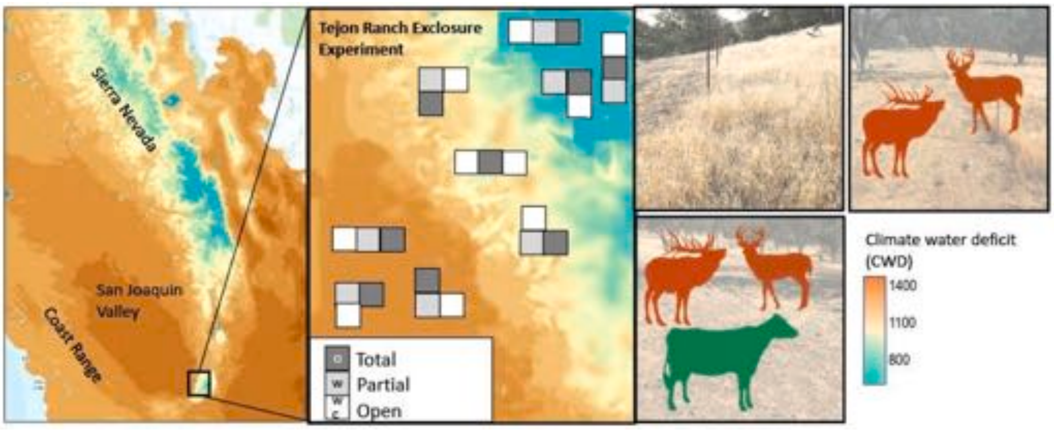

Fig. 1. Exclosure block design and overview map of large herbivore treatments used in the Tejon Ranch Exclosure Experiment (TREE). Each of the nine blocks consists of three 1 ha (100 m × 100 m) plots, each with a different treatment: open plots which are unfenced and accessible to all large herbivores; partial exclosures with fencing that excludes cattle but allows access for wild large herbivores ("wildlife plots"); and total exclosures, which prevent access for all adult large herbivores ("exclosure plots"). The blocks are grouped in three aridity levels (Arid, Intermediate, Mesic) based on downscaled climate water deficit (CWD) models. Arid blocks are situated in foothill savanna with minimal slope. Mesic and Intermediate blocks are located in montane oak woodland on north-facing and south-facing slopes, respectively.

climate levels, we performed ANOVA tests on ground cover and fractional canopy cover (data from Orr et al., in press, *Journal of Ecology*). All analyses were performed in R (R Core Team, 2020), and models were called with the “glmmTMB” package (Brooks et al., 2017). Diagnostic tests of uniformity, dispersion, and outliers were performed with the “DHARMa” package (Hartig, 2020), and we used the “emmeans” package (Lenth, 2020) to test model effect sizes and for post-hoc pairwise comparisons between effect levels.

3. Results

3.1. *Understory and canopy structure*

In the arid climate level, the understory community is dominated by invasive annual brome grasses (*Bromus diandrus* and *B. hordeaceus*); at the intermediate level, brome grass and rubber rabbitbrush (*Ericameria* nauseosa), a native woody shrub; and at the mesic level, Sierra gooseberry (*Ribes roezlii)*, a thorny native shrub, and cleavers (*Galium aparine*), an annual native forb (see Orr et al., in press, *Journal of Ecology,* for a full description of the understory community). Ground cover did not vary significantly between climate levels ($p = 0.10$). Fractional canopy cover did vary between climate levels ($p < 0.01$), with a mean canopy cover of 27.5 percent (SD = 11.0) in the arid level, 36.2 percent (SD = 10.8) in the intermediate level, and 44.9 percent (SD = 11.1) in the mesic level.

3.2. *Seedling abundance*

Abundance of seedlings (Fig. 2) was not significantly different between climate levels or herbivore treatments, nor was it explained by the interaction of these two factors (Table 1). Total exclosures in the intermediate climate level did, however, have a higher abundance of seedlings than total exclosures in the mesic climate level ($p < 0.05$).

Table 1

(a) Summary of parameters from the GLMM of total seedling abundance with a negative binomial error distribution. The random effects structure included transect nested within replicate block nested within climate level. (b) Mean and standard error of total seedling abundance for each of the nine climate level/herbivore treatment combinations. Results are averaged across nine 100 m^2 belt transects.

a)

Fixed Effects	*Incidence Rate Ratios*	*Std. Error*	*z value*	*p*
Count Model				
Intercept	0.83	0.32	−0.49	0.627
Climate Level: Intermediate	2.32	1.10	1.79	0.074
Climate Level: Mesic	0.78	0.38	−0.52	0.604
Herbivore Treatment: Wildlife	0.91	0.33	−0.26	0.792
Herbivore Treatment: Open	0.26	0.27	−1.32	0.187
Intermediate * Wildlife	0.62	0.28	−1.04	0.296
Mesic * Wildlife	0.52	0.34	−1.00	0.316
Intermediate * Open	1.42	1.57	0.31	0.753
Mesic * Open	0.00	0.00	−0.01	0.994
Observations	1338			

b)

	Arid	Intermediate	Mesic
Exclosure	1.829 ± 1.112	3.107 ± 4.524	1.923 ± 1.353
Wildlife	1.885 ± 1.327	2.273 ± 3.879	1.771 ± 1.945
Open	1.602 ± 1.000	1.836 ± 1.398	1.296 ± 0.703

3.3. *Seedling mortality*

Seedling mortality (Fig. 3) increased with aridity, with the arid climate level having a higher proportion of dead seedlings than both the intermediate level ($p < 0.001$, Table 2) and the mesic level ($p < 0.001$), and the intermediate level having higher mortality than the mesic level ($p < 0.01$). When averaged across climate levels, total exclosures had higher mortality than wildlife plots ($p < 0.001$) and open plots ($p < 0.001$), although this trend was primarily driven by the differences in mortality between herbivore treatments in the arid level. There was no significant difference in mortality between wildlife and open plots across climate levels. Within the arid climate level (Table 3), total exclosures had higher mortality than wildlife plots ($p < 0.001$) and open plots ($p < 0.001$), and there was no significant difference in mortality between wildlife and open plots.

3.4. *Living seedlings*

Abundance of living seedlings (Fig. 4) was lower in the arid climate level than in the intermediate ($p < 0.001$) or mesic ($p < 0.001$) climate

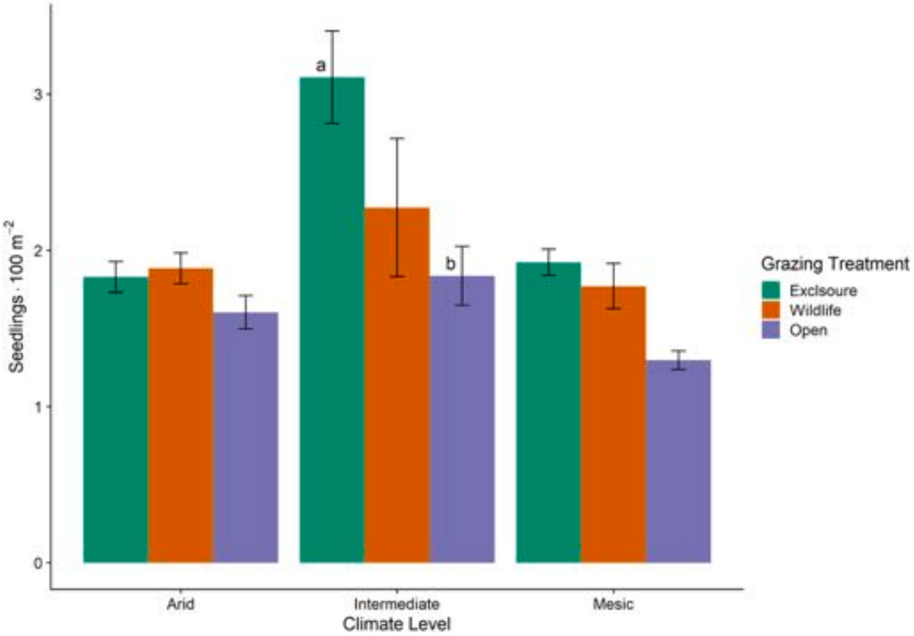

Fig. 2. Density of all seedlings (alive and dead) in each climate level, subset by herbivore treatment. Results are averaged across the nine belt transects within each climate level/treatment combination. Error bars represent the standard error of the mean. Unique letters above bars represent significantly different values ($p < 0.05$) between herbivore treatments within each climate level, from the pairwise comparison of estimated marginal means. Average values were not significantly different between climate levels.

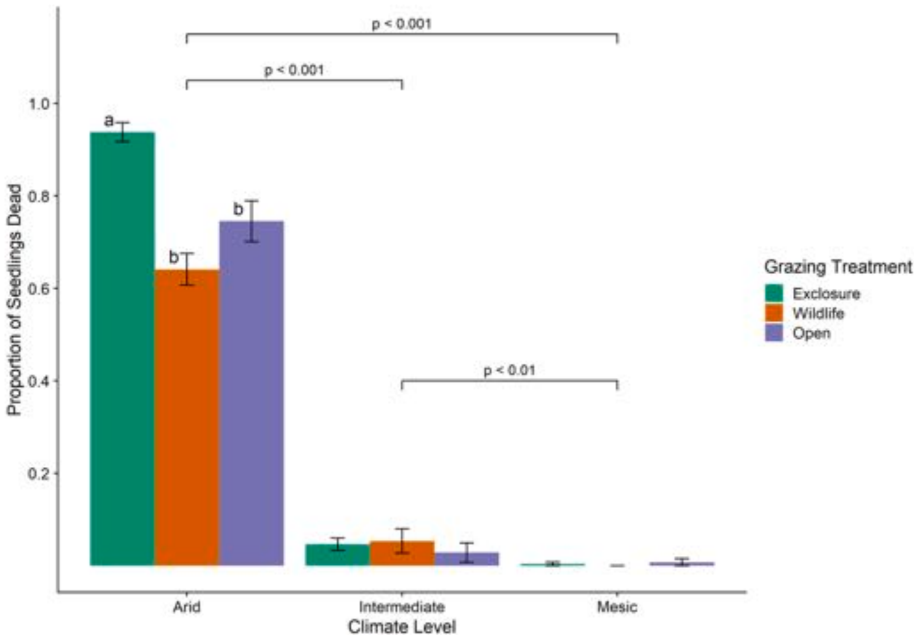

Fig. 3. Mortality of seedlings in each climate level, subset by herbivore treatment. Results are averaged across the nine 100 m^2 belt transects within each climate level/herbivore treatment combination. Error bars represent the standard error of the mean. Horizontal bars show the pairwise comparison of estimated marginal means between each climate level. Unique letters above bars represent significantly different values ($p < 0.05$) between herbivore treatments within the arid climate level, from the pairwise comparison of estimated marginal means.

Table 2

(a) Summary of parameters from the GLMM of seedling mortality with a binomial error distribution. The random effects structure included transect nested within replicate block nested within climate level. (b) Mean and standard error of seedling mortality for each of the nine climate level/herbivore treatment combinations. Results are averaged across nine 100 m^2 belt transects.

a)

Fixed Effects	*Odds Ratios*	*Std. Error*	*z value*	*p*
Intercept	20.97	16.08	3.97	**<0.001**
Climate Level: Intermediate	0.00	0.00	−5.17	**<0.001**
Climate Level: Mesic	0.00	0.00	−6.94	**<0.001**
Herbivore Treatment: Wildlife	0.19	0.06	−5.54	**<0.001**
Herbivore Treatment: Open	0.25	0.09	−4.05	**<0.001**
Observations	2712			

b)

	Arid	Intermediate	Mesic
Exclosure	0.938 ± 0.234	0.046 ± 0.206	0.004 ± 0.062
Wildlife	0.641 ± 0.461	0.053 ± 0.226	0.000 ± 0.000
Open	0.745 ± 0.416	0.028 ± 0.152	0.007 ± 0.086

Table 3

Summary of parameters from the GLMM of seedling mortality in the arid climate level with a binomial error distribution. The random effects structure included transect nested within replicate block.

Fixed Effects	*Odds Ratios*	*Std. Error*	*z value*	*p*
Intercept	27.42	19.24	4.72	**<0.001**
Herbivore Treatment: Wildlife	0.12	0.04	−5.65	**<0.001**
Herbivore Treatment: Open	0.16	0.07	−4.39	**<0.001**
Observations	720			

levels (Table 4). Wildlife plots had more living seedlings than both total exclosure plots ($p < 0.001$) and open plots ($p < 0.05$). In the arid climate level, total exclosures had fewer living seedlings than wildlife plots ($p < 0.001$) or open plots ($p < 0.001$), while in the mesic level, open plots had fewer living seedlings than total exclosures ($p < 0.001$) and wildlife plots ($p < 0.01$). Within the intermediate climate level, herbivore treatment did not have a significant impact on the number of living seedlings.

3.5. *Browse damage*

Seedlings in the arid climate level had a lower prevalence of browse damage (Fig. 5) than seedlings in the intermediate level ($p < 0.05$, Table 5) or the mesic level ($p < 0.01$). The intermediate and mesic levels did not have a significantly different prevalence of browse damage. Open plots had a higher prevalence of browse damage than total exclosures ($p < 0.001$) and wildlife plots ($p < 0.001$). Total exclosures and wildlife plots did not differ significantly in their occurrence of mortality.

4. Discussion

An understanding of how climate and herbivory influence oak seedling dynamics is key to managing oak woodlands. Our results show that seedling establishment and survival are dependent on both climatic context and large herbivores, but with important context-specific variation that could be key to developing local-level management and restoration plans. Specifically, in the two cooler, wetter climate levels, where there was a higher prevalence of browsing damage, the presence of cattle had a negative effect on the abundance of seedlings. On the other hand, in arid conditions with prevalent desiccation, large herbivores at the proper density may provide some benefit to oak seedling germination and survival – potentially by reducing the plant species which compete with seedlings for limited water (Gordon et al., 1989; Hayes and Holl, 2003).

Large herbivores had a context-specific effect on seedlings: cattle reduced total and living seedling abundance in the intermediate and mesic climate levels, respectively, while in the arid level, large herbivores were associated with increased establishment. In the absence of cattle, increases in grass cover and biomass – driven largely by invasive brome grasses – may increase shading and moisture at the soil surface early in the seedling growing season (Orr et al., in revision; Orr et al., in review). Oak germination and emergence occur largely before grasses begin to deplete water resources (Jackson and Roy, 1986; Tyler et al., 2006), so this microhabitat effect may lead to more successful oak germination (Tyler et al., 2002). However, we also found that in the absence of large herbivores, seedlings in the arid level had higher mortality rates by the end of the spring. Interestingly, the increase in invasive grass cover that is a potential benefit to seedling emergence in

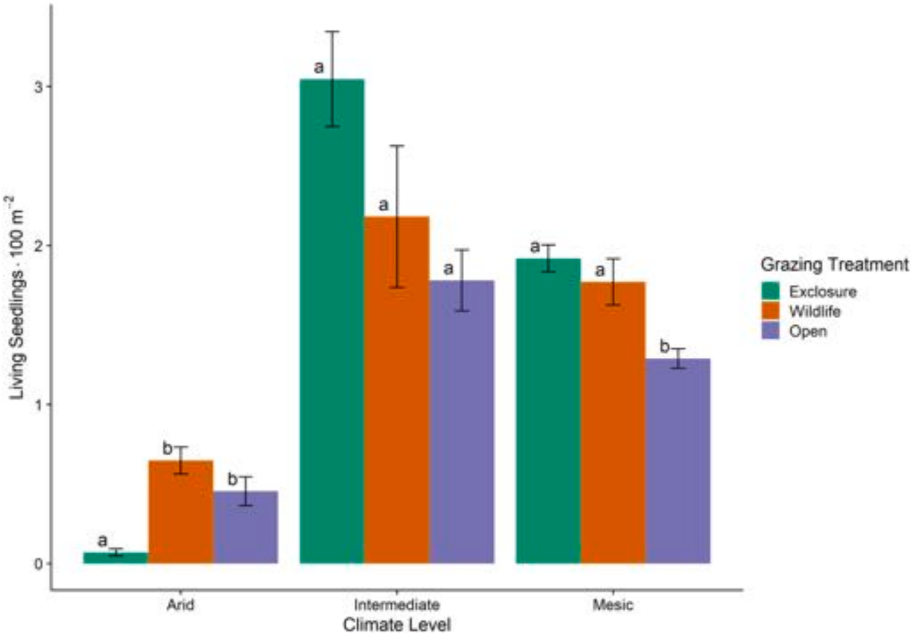

Fig. 4. Density of living seedlings in each climate level, subset by herbivore treatment. Results are averaged across the nine 100 m^2 belt transects within each climate level/treatment combination. Error bars represent the standard error of the mean. Unique letters above bars represent significantly different values ($p < 0.05$), from the pairwise comparison of estimated marginal means.

Table 4
(a) Summary of parameters from the GLMM of living seedling abundance, with a negative binomial error distribution. The random effects structure included transect nested within replicate block nested within climate level. (b) Mean and standard error of living seedling abundance for each of the nine climate level/herbivore treatment combinations. Results are averaged across nine 100 m^2 belt transects.

a)

Fixed Effects	*Incidence Rate Ratios*	*Std. Error*	*z value*	*p*
Intercept	0.08	0.03	−6.24	**<0.001**
Climate Level: Intermediate	29.05	13.28	7.37	**<0.001**
Climate Level: Mesic	22.07	9.87	6.92	**<0.001**
Herbivore Treatment: Wildlife	6.25	2.24	5.10	**<0.001**
Herbivore Treatment: Open	4.64	1.79	3.98	**<0.001**
Intermediate * Wildlife	0.12	0.05	−5.53	**<0.001**
Mesic * Wildlife	0.16	0.06	−5.01	**<0.001**
Intermediate * Open	0.13	0.06	−4.61	**<0.001**
Mesic * Open	0.14	0.06	−4.84	**<0.001**
Observations	1338			

b)

	Arid	Intermediate	Mesic
Exclosure	0.070 ± 0.256	3.047 ± 4.554	1.919 ± 1.358
Wildlife	0.648 ± 1.141	2.182 ± 3.906	1.771 ± 1.945
Open	0.455 ± 0.856	1.782 ± 1.423	1.289 ± 0.711

plots without cattle may have also contributed to increased mortality in plots without any large herbivores. Compared to native perennial grasses, exotic annual grasses have been shown to have a detrimental effect on seedling survival by depleting soil moisture throughout the growing season (Tyler et al., 2006), so the reduction of invasive grasses by large herbivores may increase available groundwater for seedlings. The arid level was dominated by invasive brome grasses, so the large herbivore-facilitated reduction in competition between seedlings and grasses may have been most significant in this climate level.

Climatic context itself also had a large effect on seedling survival, with mortality rates ranging from 42.0 to 100 percent in any given plot in the arid site, compared to between 0 and 50.0 percent in intermediate plots and 0 to 2.4 percent in mesic plots. This suggests that seedling survival in currently mesic areas may be less affected by drier climate regimes in the future, while intermediate areas may be closer to a climate-mediated "tipping point" of higher mortality as their climate comes to resemble that of currently arid regions (Coop et al., 2020; Nobre and Borma, 2009). The reduction in the number of surviving seedlings in the most arid plots compared to other climate zones highlights that this increased mortality is limiting to the abundance of oak seedlings in these sites. Therefore, seedling mortality may drive reduced recruitment and local redistribution of oak species as climate changes (Davis et al., 2016b; Dingman et al., 2013). Water stress was potentially the driving factor behind seedling mortality. We observed relatively low rates of browsing damage and a high prevalence of desiccation in the arid climate level (Fig. S3), consistent with the 2017–2018 rainy season having lower than normal precipitation. Water stress in areas predicted to have less precipitation under climate change has also been implicated as a mechanism for seedling mortality in forest ecosystems in Europe (Frei et al. 2018; Bolte et al., 2016).

Climate-mediated differences in oak stand and understory composition may explain the differential outcomes for seedlings across climate levels and herbivore treatments. For example, the higher occurrence of browsing damage in the mesic climate level could be due to black oak, which is more common in the mesic climate level, being more palatable to large herbivores than valley or blue oak. In this way, the dependence of large herbivore effects on climate level in our study could have been the result of oak stand composition differing between levels, rather than a direct effect of climatic factors. Evergreen oaks such as coast live oak (*Q. agrifolia*) may be less palatable to herbivores than deciduous species (Griffin, 1971; Perea et al., 2017), but to our knowledge, no studies have identified a difference in palatability between the three deciduous species in our study. Furthermore, seedlings of the white (Leucobalanus) and red (Erythrobalanus) oak groups vary in their responses to light and drought (Brose and Rebbeck, 2017; Rebbeck et al., 2011; Seidel, 1972), and canopy and understory structure may have influenced these two factors. Importantly for our study, blue oak is more tolerant of shade than valley oak (Callaway, 1992a; Muick, 1991) and may derive more of a benefit from the facilitative effect of shrub canopies (Callaway,

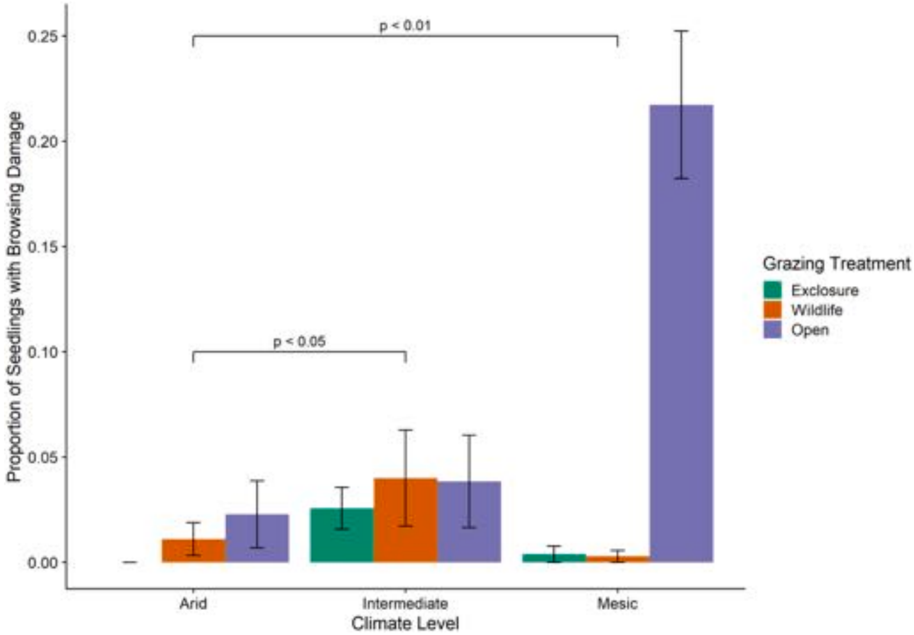

Fig. 5. Proportion of seedlings with browsing damage in each climate level, subset by herbivore treatment. Results are averaged across the nine 100 m^2 belt transects within each climate level/treatment combination. Error bars represent the standard error of the mean. Horizontal bars show the pairwise comparison of estimated marginal means between each climate level. The intermediate and mesic climate levels did not differ significantly.

Table 5

(a) Summary of parameters from the GLMM of herbivory damage, with a binomial error distribution. The random effects structure included transect nested within replicate block nested within climate level. (b) Mean and standard error of herbivory damage for each of the nine climate level/herbivore treatment combinations. Results are averaged across nine 100 m^2 belt transects.

a)

Fixed Effects	*Odds Ratios*	*Std. Error*	*z value*	*p*
Intercept	0.00	0.00	−9.83	**<0.001**
Herbivore Treatment: Wildlife	1.51	0.78	0.80	0.426
Herbivore Treatment: Open	28.78	13.07	7.40	**<0.001**
Climate Level: Intermediate	6.38	4.42	2.68	**0.007**
Climate Level: Mesic	7.27	4.59	3.14	**0.002**
Observations	2648			

b)

	Arid	Intermediate	Mesic
Exclosure	0.000 ± 0.000	0.026 ± 0.152	0.004 ± 0.062
Wildlife	0.011 ± 0.105	0.040 ± 0.197	0.003 ± 0.037
Open	0.023 ± 0.150	0.038 ± 0.160	0.217 ± 0.407

1992b). Therefore, the relative scarcity of shrubs and lower canopy cover in the arid climate level, where blue oak was more common, could have contributed to that level's higher mortality.

Furthermore, increased temperature results in advanced seedling phenology for a diverse range of tree species (Vitasse et al., 2013; Vitasse et al., 2011), and, for oaks, this effect is variable across species and can lead to increased mortality (Morin et al., 2010). Phenology may have affected the duration of exposure to browse damage and water stress faced by seedlings in each climate level in our study. Namely, advanced vegetative phenology in seedlings in the arid level may have left them more susceptible to drought, and therefore resulted in higher desiccation and mortality. While differences in phenological response between the three species of oak in our study are unclear, blue oak, which is common in the arid level, has been demonstrated to exhibit advanced phenology under increased temperature (McBride et al., 1997), consistent with the high mortality observed in the arid level. Determining the role of oak species identity in the climate-mediated impact of large herbivores on seedling establishment requires further investigation directly comparing the outcomes between oak species.

Additionally, the differences between the two large herbivore treatments, especially the increase in living seedling abundance in wildlife-only plots compared to wildlife-and-cattle plots in the arid climate level, may be due to herbivore density and not herbivore identity per se. Cattle contributed to higher browsing damage to seedlings than wildlife alone, which did not increase browsing damage above the levels seen in the total exclosure treatment – suggesting that wild herbivore densities may have been too low to have a detrimental impact on oak seedlings. Therefore, it may be the case that wild herbivores at higher densities than those of Tejon Ranch would have similar negative impacts as cattle (via elevated browsing damage), and conversely, reducing cattle densities below a certain threshold could result in enhanced seedling recruitment. Another density-dependent impact of large herbivores on oak seedlings may come through the direct consumption of acorns. Cattle and other large herbivores including deer and elk can significantly deplete acorn resources (Barrere et al. 2020, Herrera, 1995). Therefore, the difference in seedling abundance between exclosure plots and open plots, but not plots with wildlife alone, could be due to the higher density of large herbivores having a more significant role in reducing the number of acorns available for germination. Finally, despite the similar levels of browsing damage to seedlings in total exclosures and wildlife plots, we saw more seedlings in wildlife plots than in total exclosures in the arid climate level. This finding suggests that the presence of wild large herbivores at a certain density, and not just the absence of cattle, has indirect effects which are beneficial for seedling establishment and survival. Determining the mechanisms of these indirect effects, and the population densities at which they are optimal for seedling outcomes, is an avenue for further investigation into the importance of wild large herbivore population management in supporting oak recruitment.

There are many effective approaches to oak restoration, including acorn planting and caging individual seedlings to protect them against large herbivores, which are currently being tested and implemented in California's oak woodlands (Bernhardt and Swiecki, 1997; Costello et al., 1996; McCreary, 2010; McCreary and Tecklin, 1997). Other suggested methods for reducing seedling mortality include promoting the growth of shrubs, which may have a facilitative effect on oak seedlings (Callaway, 1992b; Callaway and D'Antonio, 1991) and fencing to reduce herbivory by rodents (López-Sánchez et al., 2019; Smit et al., 2008). Furthermore, there is evidence that management actions may have interactive and unintended effects, such as canopy gap creation increasing browsing damage and amplifying the benefit of protective fencing (Barrere et al., 2021). This study provides insight into how and where these targeted approaches, in conjunction with landscape-level management of large herbivores, should be applied. The effect of climate on mortality suggests that planting-based restoration of oaks may be both most necessary – and most challenging – in arid climates where establishment is low and mortality is high. Extrapolating from the relationship between aridity and seedling establishment, furthermore, suggests that currently arid regions will be most in need of management and restoration interventions in the future. Intermediate regions, meanwhile, may experience a much greater increase in mortality than currently mesic sites, so the former should be prioritized when allocating resources to enhance seedling survival. Furthermore, the effect of cattle on living seedling abundance shifted from detrimental, to neutral, to beneficial as climate became warmer and more arid, suggesting that livestock management should adapt as climate change progresses. Our results also highlight the need to better understand and utilize the local adaptations of genetically distinct oak populations to ensure the long-term success of restoration efforts, as interspecific variation in seedling climatic tolerance has been demonstrated in California (Rice et al., 1997; Sork et al., 2010) and across Europe, Asia, and Central America (Flores et al., 2018; Richter et al., 2012; Cregg and Zhang, 2001). Further research should also seek to determine how oak stand composition varies across climatic contexts, and how oak species identity modulates the effects of herbivory by large herbivores.

However, the restoration measures described above are not always feasible, especially at large scales. If no direct interventions to promote establishment or survival are made, the best large herbivore regime for enhancing seedling outcomes is one that does not include cattle, but may include wildlife depending on the climate and associated flora, as well as the densities at which large wild herbivores occur. The arid climate level was the only level in which the presence of wildlife seemed to provide a benefit to seedling survival, possibly due to the aforementioned effects of grazing on understory plant communities in a way that favors oak seedlings (e.g., reduced competition and increased soil moisture), but also potentially because of oak stand composition varying across climate levels and the aforementioned differences between oak species. This finding may explain why oak species in mixed forests benefit less from the exclusion of deer than other tree genera (Laurent et al., 2017). However, wildlife did not increase browsing damage on seedlings, but cattle did, as there were roughly ten times as many seedlings with browsing damage in open plots than in wildlife plots or total exclosures. This is a potential mechanism for higher living seedling abundance in exclosures than in open plots and supports previous findings that large wildlife does not impact seedlings as much as cattle (López-Sánchez et al., 2019; Perea et al., 2017; Smit et al., 2008), suggesting that fencing may not provide much benefit for oaks in sites where cattle are absent. Indeed, browsing damage was inversely related to CWD, further validating the use of large wild herbivores in a restoration context in arid climates. Oak recruitment may therefore benefit from both local livestock exclusion and practices to promote large wildlife populations (California Department of Fish and Wildlife, 2018; Loft and Bleich, 2014; Tietje et al., 2005). However, this management strategy is dependent on the preexisting density of wild large herbivores, due to the aforementioned potential for high densities of wild large herbivores to increase browsing damage. Additionally, the benefit that seedlings confer from the presence of wild herbivores as a result of the grazing of competing species may not be sufficient at lower population densities. It is also important to note that in our sites, belowground herbivory (assumed to be from California ground squirrels, *Otospermophilus beecheyi*) only occurred in the most arid climate level, providing an alternative mechanism for increased mortality (Fig. S4). Large herbivores have been shown to limit rodent populations (Muñoz et al., 2009; Pulido and Díaz, 2016; Smit et al., 2001), so the beneficial presence of wildlife on seedling establishment and survival could also be due to the exclusion of belowground herbivores.

California's oak-dominated ecosystems face an uncertain future due to anthropogenic impacts on both climate and large herbivore regimes (Byrd et al., 2015; Sleeter et al., 2011). Our results indicate that management practices must consider not only how large herbivores affect oak seedlings, but how these effects may change over time due to climate change. We observed that oak seedling outcomes vary much more between the 50-year and 100-year climate scenario than between the present-day and 50-year scenario. This phenomenon suggests a "tipping point" of oak establishment decline, with implications for entire ecosystems if a certain climatic threshold is crossed – potentially leading to alternative ecological states (Suding et al., 2004). Management of sustainable oak populations, therefore, must include the identification of at-risk areas and the determination of site-specific factors preventing recruitment. Applied management of large herbivores, taking into account both ecological context and changing climatic conditions, is a valuable tool for preventing further loss of endemic oak ecosystems in California and around the globe.

CRediT authorship contribution statement

John Parsons: Data curation, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Carina Motta:** Conceptualization, Investigation, Writing – review & editing. **Garima Sehgal:** Investigation, Writing – review & editing. **Ana Miller-ter-Kuile:** Formal analysis, Writing – original draft, Writing – review & editing. **Hillary Young:** Funding acquisition, Project administration, Supervision, Conceptualization, Resources, Writing – review & editing. **Devyn Orr:** Funding acquisition, Project administration, Supervision, Resources, Conceptualization, Investigation, Formal analysis, Visualization, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

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