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Escaping the Browse Trap: Patterns of Natural Blue Oak Regeneration in Grazed Landscapes

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A R T I C L E I N F O

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A B S T R A C T

Blue oak, *Quercus douglasii*, are vital components of California's foothill ecosystems. Widespread oak recruitment failure has led to considerable restoration efforts, with mixed success. Natural regeneration is hindered at least in part by extensive cattle grazing, resulting in a troubling recruitment gap in many natural populations. Despite this, certain areas within ranches exhibit natural oak recruitment, suggesting the existence of conditions compatible with both grazing and oak regeneration. Understanding these conditions is essential for developing sustainable conservation and rangeland management practices. We conducted a comprehensive survey of 24 active cattle ranches across Northern California to identify factors influencing oak recruitment and to attempt to propose a range of optimal grazing pressures for natural blue oak recruitment. We found that rocky refugia with reduced grazing pressure were associated with greater oak recruitment. Low cattle presence, rockiness, low herbaceous cover, and high shade all significantly predicted oak recruitment sites. Tree-ring analysis revealed that saplings exhibited extremely variable growth rates, but slower under high grazing pressure, indicating the presence of a "browse trap," from which saplings struggle to escape cattle browse. Achieving sustainable oak regeneration may require at least temporarily reducing grazing pressure or implementing other grazing strategies to facilitate oak recruitment and enable saplings to pass through the browse trap. Our results underscore the critical role of landscape conditions and cattle management in supporting oak recruitment refugia. These findings have practical implications for land management, highlighting the importance of balancing grazing practices with conservation efforts to ensure the long-term health and biodiversity of oak woodlands in California's Central Valley foothills.

Introduction

Blue oaks (*Quercus douglasii*) are a cornerstone of the foothill ecosystems encircling California's Central Valley. Blue oak woodlands account for one-third of the grazed land in California and harbor more wildlife than any other ecosystem in the state (Borchert et al. 1991; Pavlik et al. 1991). However, the ability of blue oaks to regenerate under current land use practices, largely characterized by cattle grazing, is in doubt. Many foothill cattle ranches show little to no recruitment of blue oaks, as evidenced by the lack of multiple age classes in oak populations (McClaren and Bartolome 1989; Adams et al 1991, Swiecki and Bernhardt 1997; Davis et al. 2016). Despite this overall trend, small refugia on multiple ranches exhibit visible oak seedlings and saplings (Palmerlee and Vaughn, personal observation), indicating that natural oak recruitment is possible under certain conditions.

Because natural recruitment is scarce, restoration efforts for establishing blue oaks have often focused on planting techniques that control for various limiting factors, such as using container stock, irrigation, tubes, and fencing (Brooks and Merenlender 2001; Young and Evans 2005). However, these techniques are often expensive and impractical for large-scale restoration projects and may not be sufficient to mitigate the potential loss of extant oak woodlands (Standiford et al. 2002). Experimental, large-scale replanting techniques have also concluded that, within extant woodlands, management solutions are likely more cost-effective (Palmerlee and Young 2022).

Recent studies have emphasized the need for further research on the conditions that would ensure tree regeneration in California rangelands, particularly in determining thresholds of grazing density and timing (Lopez-Sanchez et al. 2014). While many fac-

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tors, such as nurse plants, annual grasses, rodents, deer, climate change, and fire, can limit oak recruitment (McCreary 2001, Tyler et al. 2008), grazing pressure appears to be a critical factor affecting oak regeneration in many areas.

Despite the potential benefits of grazing in maintaining open landscapes and reducing the risk of wildfire, excessive grazing pressure can impede oak regeneration by directly damaging seedlings and saplings, both from trampling and direct consumption (Leal et al. 2022). Grazing impacts can be complex, as grazing can reduce competition from other plants or eliminate habitat for rodent herbivores, which can benefit oak seedling survival in some cases (Adams et al. 1991; Bernhardt and Swiecki 1997; Tyler et al. 2006). However, in many instances, cattle browsing can significantly reduce the likelihood of seedling establishment and prevent young oaks from reaching heights sufficient to escape further herbivory or susceptibility to fire (Allen-Diaz and Bartolome 1992; Holmes et al. 2011). This phenomenon, known as a “browse trap” (cf., Staver and Bond 2014), effectively creates trees incapable of reaching reproductive maturity due to repeated grazing.

Several studies have highlighted the challenge of finding a balance in grazing management that promotes oak regeneration while maintaining other ecosystem functions. For example, cattle grazing has been shown to have both positive and negative effects on oak seedling survival, highlighting the complexity of interactions between herbivores, climate, and vegetation in these ecosystems (Reiner and Craig 2011; Smith et al. 2020; Brown et al. 2021; Parsons et al. 2021; Garcia et al. 2022; Leal et al. 2022). These findings all suggest that a nuanced approach to grazing management is necessary to promote natural oak regeneration in California’s oak woodlands.

Considering these challenges, our study aimed to identify factors associated with natural oak recruitment on cattle ranches in Northern California. Our central hypothesis was that natural oak recruitment occurs in areas where grazing pressure is artificially reduced by landscape conditions; that these recruitment refugia exist because physical factors are creating pockets of low grazing intensity relative to the rest of the ranch. In order to test this hypothesis, we surveyed over 20 cattle ranches, finding and sampling natural oak recruitment locations, to better understand the relationship between cattle management and oak recruitment patterns.

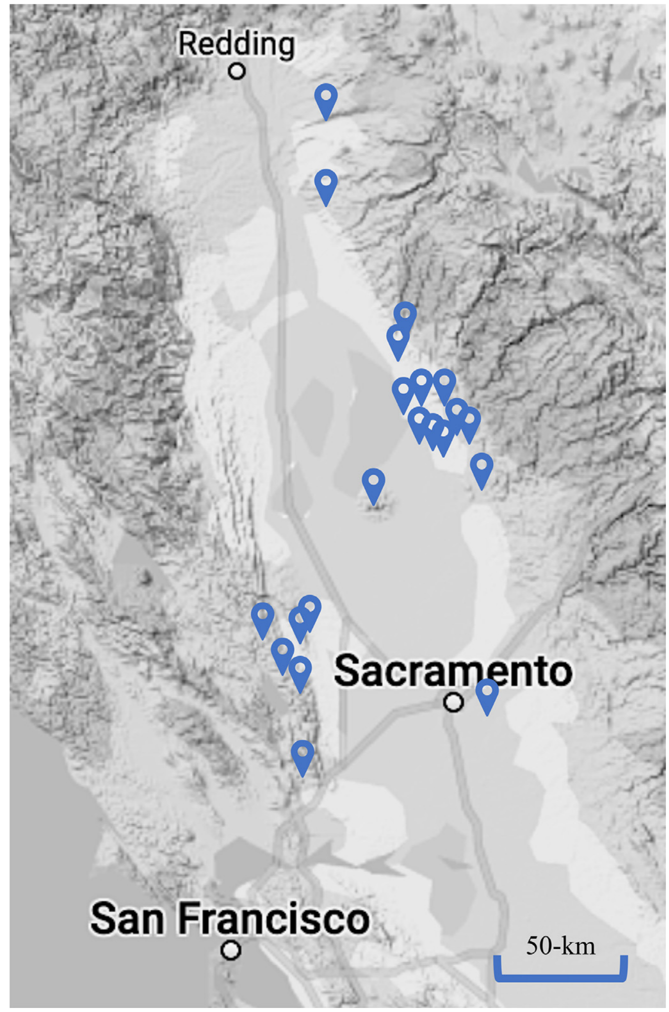

Figure 1. Participating ranches located on both east and west sides of California’s Central Valley, as well as within the Sutter Buttes, between 30 and 450 m in elevation.

Study Area and Methods

Study area

The study was conducted in the foothills surrounding Northern California’s Central Valley, on cattle ranches (Fig. 1) between 30 and 450 m in elevation. Ranches were all dominated by the open blue oak woodland that is typical of the region: an overstory of nearly ubiquitous blue oak cover and an understory dominated by annual grasses. The ranches participating in the study were selected from researchers’ existing landowner networks, through landowner-to-landowner referral, by nonprofit partners working on private lands (Audubon California and Point Blue Conservation Science), and via connections from local agencies (Resource Conservation Districts and Natural Resource Conservation Service offices). Ranch rangelands were all currently grazed by cattle. Specific grazing management, including duration, intensity, and pasture rotations, varied ranch to ranch.

Field data collection

In the fall of 2022, we surveyed 24 cattle ranches for visible oak recruitment. Ranches varied in size from 150 to 20,000 hectares. The goal was not an exhaustive survey of each ranch, but rather to capture a picture of natural oak recruitment within each ranch. In order to not oversample a given ranch, no more than 5 recruitment sites were taken from one property. In all, we identified 60 recruitment locations across all ranches that met our criteria. Because these recruitment sites are rare, and to avoid any bias by the survey team, we relied primarily on the landowner or land manager to determine where recruits had already been seen. When a landowner was unavailable to identify recruitment locations, we used a vehicle to explore the ranch, scanning the area by eye and with a spotting scope. As surveys were conducted in early summer, all grasses were dead and small oaks were easily identified. While it is common to see many very small oaks (under 10 cm) on these ranches, (Palmerlee and Vaughn personal observation) few if any of these individuals mature. Because of this, we focused our search on individuals between 11 cm and 5 m. We did not sample any areas near a water feature in order to minimize the impact of water availability as a factor in oak recruitment.

Whenever an individual was spotted, we set out on foot and marked the location with a pin flag. From that flag, a 20 m radius circle was visually surveyed. To qualify as a recruitment area, and not an anomaly, the site needed 5 or more individuals within that circle between 11 cm and 5 m in height. We then counted the total number of individuals within the circle and the presence/absence of three height classes (seedling: 0–10 cm, sapling:

11 cm to 2 m, immature: 2.1–5 m, mature >5 m). Each area was ranked within three density classes: 5–11, 12–40, and >40 individuals/395 m^2. The total number of mature trees (>5-m in height) was also recorded within each 20-m radius. Once the 20 m radius circle was surveyed, we moved the pin flag to a new point that better represented the estimated center of the recruitment density. A 5 m radius area around this new pin flag location was then surveyed for environmental variables. A GPS waypoint was marked, a photo taken, and shade recorded as a percentage estimated by coverage at 12 noon. Slope was recorded as a percentage in three classes (0–10%, 11–30%, >30%) and aspect recorded using a compass feature on the GPS unit. Visual estimates of cover were recorded as percentages of bare ground, woody debris, rock, and herbaceous cover. The 5-m radius circle was then surveyed for cattle dung. Any piece of dung was marked with a pin flag unless the surveyor determined that several small pieces were from the same bowel movement. After two independent rounds of counting, the number of pin flags was recorded. We then converted this measurement into a standard number of dung per square meter.

This combination of using a 20 m circle and a 5 m subcircle was important for both practical reasons and to prevent surveyor bias. In order to survey with minimal bias for a rare phenomena across large spatial areas, we settled on establishing the center of the 20 m sampling area on the first individual we saw. However, upon seeing the site up close, if it was clear that the concentration of the recruitment phenomena was occurring in one quadrant of that 20 m circle, then we adjusted the center for the smaller 5 m radius sampling. Sampling in a 5 m radius circle was also more practical for our dung counts.

A destructive sample was taken to determine the relationship of height to age. To limit bias, we selected the nearest individual to the center pin. That individual's height was recorded, it was cut down at ground level, and the stem marked with a metal tag corresponding to the ranch and recruitment area. In the case of a tree with many stems, care was taken to sample below the point where all sprouts originated, or the tree was bypassed and we cut down the next closest seedling. Samples were dated under microscope at the Tree-Ring Laboratory at the University of Arkansas, Fayetteville.

After the recruitment area was sampled, we located an adjacent paired "non-recruiting" site. In order to find an unbiased paired site, surveyors walked due north for 100 m using a GPS compass feature. A pin flag was set down and a 20 m radius circle was surveyed to determine if there were any recruiting individuals. If there were less than 5 blue oaks between 11 cm and 5 m in height, the location was surveyed using the same methods described above. If there were 5 or more recruited individuals, the site was considered part of the original recruitment area and surveyors went back to the original center of the recruitment area, turned east, and paced out 100 m. If recruits were still encountered, surveyors returned to center and turned south. If 5 or more recruits were found at 100 m of every cardinal direction, the same protocol was expanded to 200 m until an area was found with fewer than 5 recruited oaks. Furthermore, in order to maintain similarity between recruitment areas and the nonrecruiting pair, if surveyors encountered a boundary or obstruction (fence, canyon, water feature) they would abandon that direction, return to center, and try the next cardinal direction.

Rancher interviews

Each participating landowner agreed to discuss their stocking rates and management practices. After surveys, a map of each ranch with the location of each sampling point was sent to landowners. An informal phone interview was conducted with the landowner or in some cases the cattle operator (whichever had more knowledge of the grazing history) (Appendix A). Because recruitment sites represented establishment often decades in the past, interviewees were asked about their current and past management and known management of past owners or grazing tenants.

One purpose of the interviews was to build a cumulative grazing score for each recruitment site and paired nonrecruitment site. We used the method described by Swiecki et al. (1997). This equation defines a cumulative grazing score as (months grazed) × (relative stocking range) × (season factor), with relative stocking ranges from 0 (none) to 3 (high). Season factor was scored as "1" for grazing only in the winter and "2" for year-round. To calculate the relative stocking rate we divided the total acreage of the pasture with the number of animals (both supplied by the landowner). With all ranches calculated, we separated ranches into low (1), medium (2), and high (3) ranges. Ranchers were also asked about any known significant fires or large changes in grazing management. There were only two ranches with high fire frequency and no grazing changes that affected the ranch's cumulative score.

Statistical analyses

All statistical analyses were performed in JASP version 0.18.3 (JASP Team 2024). We fit a Generalized Linear Mixed Model across recruiting ($n = 60$) and nonrecruiting ($n = 60$) sites with dung density as the dependent variable, and visual surface rock cover, visual herbaceous cover, and shade cover as fixed effects.

To explore what might be driving the observed difference in dung density between recruiting and nonrecruiting sites we fit a General Linear Model (GLM) with dung density as the dependant variable and visual surface rock, visual herbaceous, and shade cover as covariates across all sites. For the destructively harvested saplings we fit independent simple linear regressions for all three combinations of age, basal radial width, and height.

Finally, we derived average height growth rate from the destructive sampling and tree ring aging analysis and combined it with the scored data from our rancher interviews to fit an unbalanced ANOVA across the three grazing pressure categories (Low, $n = 19$; Mid, $n = 26$; High, $n = 15$).

Results

Biotic and abiotic predictors of recruitment status

Cattle pressure, as measured by dung density, significantly predicted blue oak recruitment sites ($P = 0.017$). Dung in sites without recruitment was nearly twice as dense as in the paired recruiting sites (Fig. 2A). Similarly, rockiness also predicted recruitment sites ($P = 0.006$). Recruiting sites were more than twice as rocky as nonrecruiting sites (Fig. 2B). Recruiting sites also were 94% shadier (Fig. 2C; $P = 0.012$) and had 12% less herbaceous cover (Fig. 2D; $P = 0.02$). Dung density was also negatively correlated with surface rockiness ($P = 0.014$) where, on average, the sites without rock (0% cover) had more than 7× denser dung than the rockiest sites (≥25% cover; Fig. 3). None of the other factors included in the GLM were significantly correlated.

Sapling age within recruitment sites

The tree ring analysis showed high variation in sapling radial growth rates over time and between individuals (Fig. 4). Age of saplings correlated strongly with basal radial width ($r^2 = 0.35$, $P < 0.001$; Fig. 5A) and significantly with height ($r^2 = 0.09$, $P = 0.02$; Fig. 5B), although with considerable variation. The oldest sapling in the sample (65 years) was only 23 cm tall, and the two tallest (>60 cm) were relatively young (20–30 years old). Height and ra-

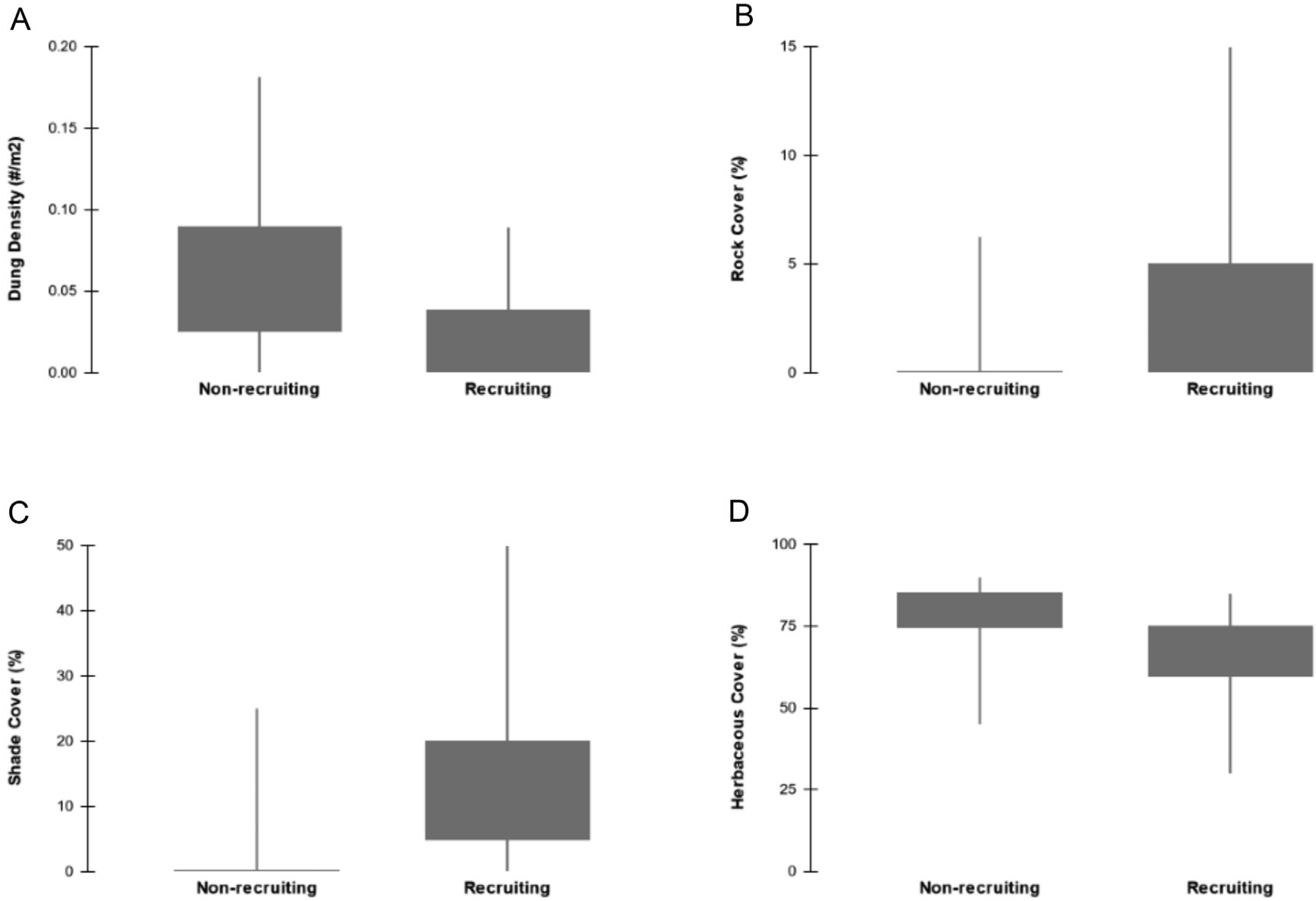

Figure 2. Field survey data showing recruiting status by number of dung density (**A**), percent surface rock cover (**B**), herbaceous cover (**C**), and percent shade (**D**). Values are means ± SE. Data collected in June of 2023. Ranches were located in Northern California between 30 and 450 m in elevation.

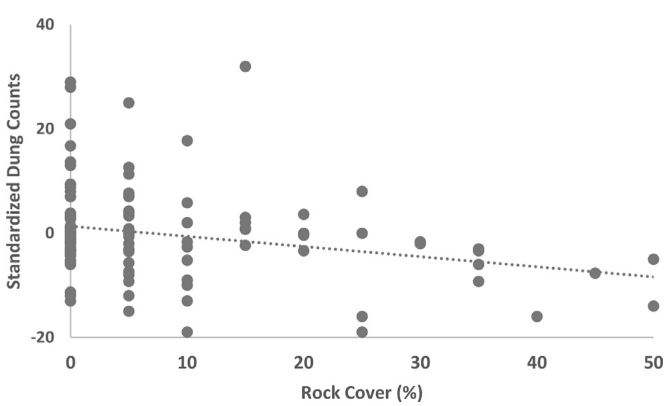

Figure 3. Field survey data showing percent surface rock cover by dung density standardized across ranches. Data collected in June of 2023 from ranches located in Northern California between 30 and 450 m in elevation.

dial width were also strongly correlated ($r^2 = 0.47$, $P < 0.001$; Fig. 5C).

Rancher-reported cattle pressure and sapling growth

When we combined data from our land manager interviews and tree ring analysis, we found on average blue oak saplings increase in height 60% faster under low grazing pressure than under higher

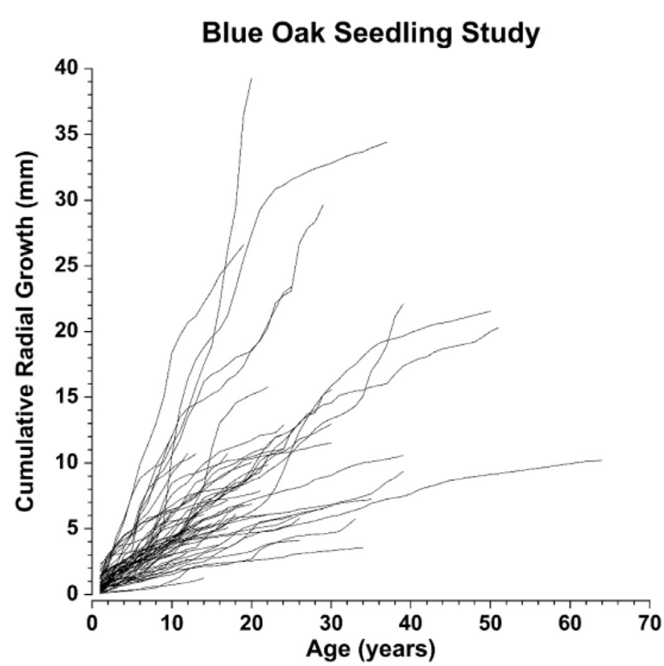

Figure 4. Tree ring analysis data showing cumulative radial growth rate over time. All samples were taken in June of 2023 from ranches in Northern California between 30 and 450 m in elevation.

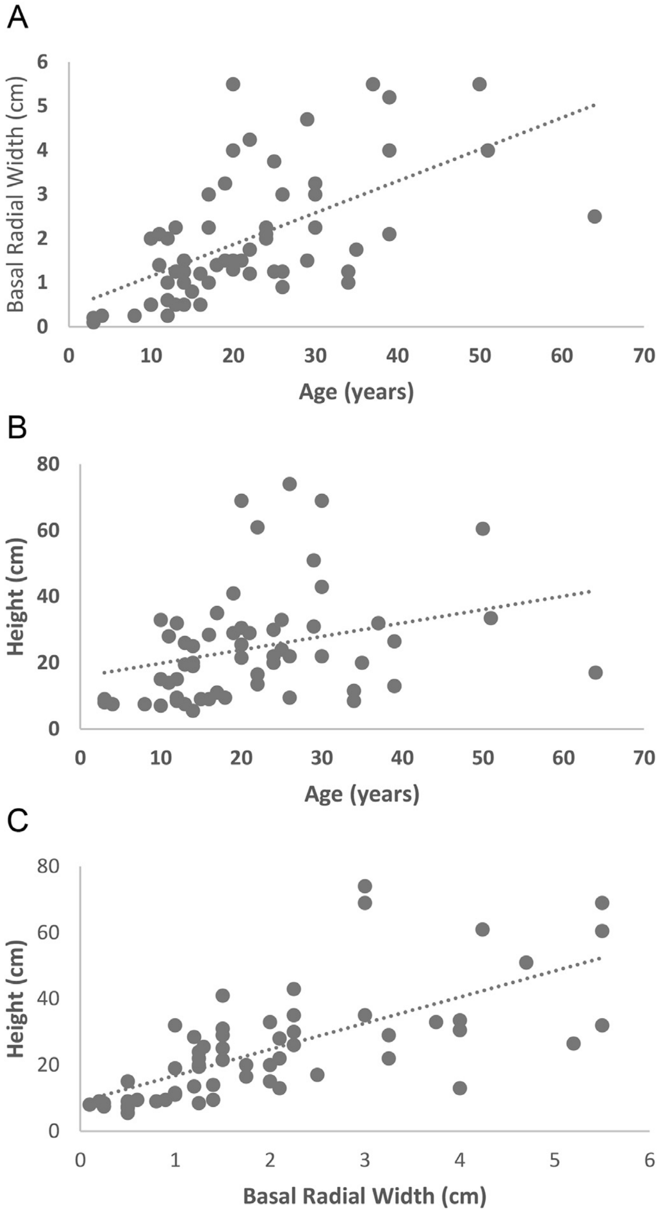

Figure 5. Tree ring analysis data showing significant correlations between age and radial width (**A**), age and height (**B**), and radial width and height (**C**). All samples were taken in June of 2023 from ranches in Northern California between 30 and 450 m in elevation.

Figure 6. Land manager survey and tree ring analysis data showing average height growth rates by grazing class. Values are means ± SE. Bars sharing a letter are not significantly different (by Tukey's HSD). Study was conducted in the summer of 2023 at ranches located in Northern California between 30 and 450 m in elevation.

Table 1
Calculations of mean (average observed growth rate), minimum (fastest observed growth rate), and maximum (slowest observed growth rate) times to release height (2 m) by cattle pressure class based on destructive samples assuming constant rates of growth throughout sapling stage.

Grazing class	Mean years to release	Min. years to release	Max. years to release
Low	113	60	509
Med/high	180	58	800

Growth rate was calculated for each destructive sample via tree-ring analyses for age and a field measurement of height. Grazing class was determined using the land-manager-provided information on stocking rate to assign a cumulative grazing [(months grazed) × (relative stocking range) × (season factor)] between 0 and 3. Ranches were then grouped as low (1), medium (2), or high (3). Data was collected in June of 2023. All ranches were located in Northern California between 30 and 450 m in elevation.

pressures ($P = 0.01$, Fig. 6). Assuming a constant rate of individual height growth throughout the sapling stage, our data show it may take a minimum of several decades, to well over a century, for individuals to reach a height above cattle pressure (~2 m; Table 1). However, saplings under lower cattle pressure would reach release height 67 years sooner, on average, than those under higher cattle pressure (Table 1). Finally, it is also notable that those individuals with the slowest growth rates are unlikely to survive the several centuries needed to reach release height (Table 1).

Discussion

Factors influencing oak recruitment

We found that dung density, rockiness, herbaceous cover, and shade cover were all significantly correlated with natural blue oak recruitment (Fig. 2). That recruitment sites are shadier seems intuitive, presumably because seedlings fare better in shade or are often in proximity to mature acorn-bearing trees (Smith et al. 2020; Brown et al. 2021; Garcia et al. 2022). That sites had less vegetation is likely correlated with the shadiness; however, our data were not strong enough to parse out interactions of these critical factors. The only factor that we found to be predictive of dung density was rock cover (Fig. 3). Young et al (2005) addressed concerns about the accuracy of dung counts as a surrogate measure of cattle presence and concluded that there was "ample evidence that when used to estimate relative habitat use within habitats and time periods, dung counts are not only reliable but more reliable than aerial or ground counts." Assuming, therefore, that our dung count are an accurate portrayal of cattle presence, the results suggest that cattle may be less likely to travel through, spend time foraging in, or to bed down to ruminate in rocky areas. While it is possible that rockiness provides other cobenefits, our data support our hypothesis that natural oak refugia exist, at least in part, due to a reduction of the relative grazing pressure of these specific areas, allowing oaks to more easily establish. Of the many factors affecting recruitment, surveyed in this study and cited in an array of manuscripts (McCreary 2001; Tyler et al. 2008), this data suggest that cattle are a strong driving force of blue oak recruitment. If, as these results suggest, rockiness reduces localized grazing pressure, there are clear implications that manipulating grazing levels can influence natural oak recruitment on a large spatial scale.

Browse trap and growth rates

Ranches with rancher-reported lower grazing pressure had faster-growing trees (Fig. 6). Many oaks struggle to clear 2-m in height, a critical threshold where they are released from browse pressure (McCreary 2010) or avoid being top-killed by fire (Holmes et al. 2011). If saplings are repeatedly browsed or otherwise damaged before reaching that height, they may become stuck in a "browse trap" (c.f. Staver and Bond 2014). Taken together, our tree-ring and interview data strongly suggest that higher grazing pressure may slow the rate at which blue oaks can escape their browse trap. For example, all saplings with a basal diameter of 1 cm ranged in age between 3 and 32 years old and one individual was 64 years old and less than half a meter tall (Fig. 4). On average, these saplings may take several decades, to well over a century, to escape their browse traps (Table 1). Given these long timeframes, many of these individuals may not survive long enough to reach maturity.

If, as our data suggest, the existence of smaller oaks in a woodland does not necessarily mean active or adequate natural regeneration, it is possible that small trees on the landscape represent a "zombie" population, one that will never reach maturity under status quo land management, and should not be considered part of a new generation of blue oaks. This possibility means that the natural regeneration of blue oak woodlands, subject of decades-long concern, could be in even worse condition than previously thought.

More work is needed to develop a picture of the full spectrum of blue oak growth rates. The aging of blue oaks is far more common among mature trees, with sampling protocols calling for coring at breast height, which doesn't capture any growth data below that height (Dr. W. Stahle, personal communication). While our aging data show a wide range of growth rates, more sampling of trees below breast height (at ground level) would provide a critical picture of the first 100 years of blue oak growth. Furthermore, sampling under multiple conditions would provide a more complete picture of a growth rate continuum. A growth rate analysis of small oaks outside of grazed areas could parse out the browse effects of cattle versus those of wildlife such as feral pigs and deer that our study did not consider. Our aging data also demonstrate that, at least in these grazing scenarios, basal diameter ($r^2 = 0.35$) is a better predictor of age than height ($r^2 = 0.09$), information that would be valuable to future research (Fig. 5).

An ideal grazing pressure

While a prescription of an ideal stocking rate compatible with natural oak recruitment is not possible from our data, they do suggest land-management options that reduce grazing intensity could be considered by landowners. As other studies have suggested (Leal et al. 2022), our results demonstrate that cattle have a direct negative impact on oak regeneration. However, previous research has indicated that complete cattle exclusion is not particularly compatible with oak recruitment (due to issues with increases in fire intensity, annual grass competition, and rodent predation (Adams et al. 1991; Bernhardt and Swiecki 1997; Tyler et al. 2006)). It seems likely that somewhere between complete rest and status quo grazing there is a stocking rate more compatible with natural oak recruitment, one that seemingly balances the conflicting results regarding the impact of cattle on young oaks. The obvious challenge is that management change away from the status quo would likely come at a (perhaps unacceptable) price to the landowner. New technologies, such as virtual fencing, could be applied at perhaps a lower cost to the landowner. Virtual fencing has been shown effective at managing cattle for fire recovery (Boyd et al. 2022) and for conservation goals in rangelands (Wätzold et al. 2024). Virtual fencing could also be used to exclude cattle from areas seasonally. Because blue oaks are winter deciduous, limiting grazing to winter months (December through February) could also prove effective. However, much of the damage to small oak trees is due to rubbing and scratching that often snaps off large leading branches (Palmerlee and Vaughn, personal observation).

Our study sheds more light on the complex relationship between cattle grazing and oak regeneration in California's blue oak woodlands. We found that shade, rockiness, and dung density were significant factors influencing oak recruitment. We identify a critical browse trap, where oak seedlings are unable to escape browsing pressure, that presents a significant challenge to oak regeneration as many saplings will require several decades, to over a century, to reach escape height under current grazing pressures. Further research is needed to determine if there are optimal grazing regimes to balance cattle grazing and sustainable oak populations. Management practices that reduce grazing intensity may not only promote natural oak regeneration on a large spatial scale but may also allow current small oaks a critical window to escape the browse trap.

Implications

- Identifying factors that support natural oak recruitment can inform targeted management practices to enhance and restore oak populations.
- Small oaks may not be young at all. In fact, many may be caught in a browse trap which effectively prevents development to mature trees. Therefore, their presence on the landscape may provide a false sense of adequate recruitment.
- Natural refugia suggest that there is a stocking rate where cattle grazing can be compatible with blue oak recruitment.

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 article.

CRediT authorship contribution statement

Alex Palmerlee: Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Kurt Vaughn:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Truman Young:** Writing – review & editing, Supervision.

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Appendix A

Landowner/land manager interviews were conducted via phone. Prior to the interview, landowners were sent a map of their property with the locations of our samples. For each pasture containing a sample, landowners were asked the following questions:

- How long have you owned/managed/leased this property?

- How many acres is this pasture?
- How many cattle are put in this pasture?
- When do cattle come into this pasture?
- When are cattle taken out of this pasture?
- Have there been any dramatic changes in the grazing management under your time at this ranch?
- Have there been any destructive events in this pasture such as fires, plowing, or mowing?
- Do you have any knowledge of the management before your tenure?

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