Title: Resprouting sustains cork oak seedlings while recent grazing limits resprouting and survival

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Abstract

1. Regeneration failure is a major bottleneck in Mediterranean oak woodlands. Cattle can hinder or promote recruitment, depending on the spatial, temporal, and intensity patterns of grazing. Herbivory theory predicts that repeated defoliation and trampling deplete seedling reserves, whereas resprouting can extend survival; yet field studies rarely separate intensity from recency or pair long-run grazing records with individual fates and microhabitat/climate context.

2. We test how management-driven heterogeneity shapes cork-oak (*Quercus suber*) seedling survival and resprouting, combining 12 years of paddock-level grazing records with individual tracking of 8431 seedlings across 24 rotational paddocks. We fitted Bayesian mixed-effects survival models relating oak seedling lifespan to grazing pressure × history (moderate ≤150; high >150 $LSU \cdot ha^{-1} \cdot days \cdot yr^{-1}$), with covariates (initial height, resprouting status, shrub distance, cattle dung counts as a proxy of very recent grazing, and 1-month SPEI as recent water balance), and Bayesian logistic mixed models relating resprouting probability to grazing treatments.

3. Survival was consistently lower in grazed than ungrazed paddocks and declined along management gradients: median lifespan fell from 460 (moderate grazing) to 256 days (high), and from 460 (old grazing; two-year exclusion) to 199 days (recent). A two-year exclusion raised survival under moderate pressure but was insufficient where pressure remained high, indicating legacy effects and that recovery windows must scale with pressure.

4. Resprouting was the dominant axis of persistence: resprouters lived >5× longer than non-resprouters (2351 vs 460 days). Taller seedlings lived longer, shrub proximity conferred a modest benefit.

5. Drought exacerbates mortality, whereas wetter recent periods (higher SPEI) markedly boosted survival. Cattle reduced the odds of resprouting, with the strongest penalty under recent use.

Synthesis. By disentangling grazing intensity from recency and linking both to seedling survival and resprouting, we show why recruitment falters under continuous, heavy grazing and when it can recover. Crucially, cattle effects are exacerbated by drought periods. Management that couples moderate stocking with multi-year rest periods—long enough to rebuild bud banks and below-ground reserves—should improve regeneration in working Mediterranean woodlands.

Keywords: Agroforestry; Herbivory; Wood-pasture; Oak woodland; Montado; *Quercus suber*; silvopastoral; Vegetative resprouting; Facilitation

1. Introduction

Regeneration is a critical bottleneck for the persistence of Mediterranean oak agroforestry systems, where seedling survival is shaped by intense biotic and abiotic filters (Harper, 1977; Pulido & Díaz, 2005; Tyler et al., 2006; Vaz et al., 2019; Díaz et al., 2021). Herbivory theory predicts that repeated defoliation and trampling curtail photosynthetic area and deplete reserves, while resprouting can restore above-ground biomass after top-kill and thus extend survival (Bond & Midgley, 2001; Clarke et al., 2013; Milios et al., 2014; Mechergui et al., 2023). Yet, in working landscapes where livestock is central, grazing can either inhibit or facilitate recruitment depending on pressure, timing, and spatial distribution (López-Sánchez et al., 2014; Schieltz & Rubenstein, 2016). Clarifying when grazing depresses versus permits early establishment—and how resprouting mediates outcomes—remains a key ecological and management question.

Mediterranean oak woodlands—such as Portuguese cork-oak (*Quercus suber*) montados and Spanish dehesas—are emblematic agrosilvopastoral systems that deliver substantial ecological and socio-economic benefits but face converging pressures from pathogens, herbivorous insects, wildfires, climate change, and management legacies (Branco & Ramos, 2009; Plieninger et al., 2015; Listopad et al., 2018; Vaz et al., 2013; Wadud et al., 2024). Cattle are globally pervasive and a dominant land use in Iberian oak systems (Carmona et al., 2013). High grazing pressure can alter community structure, soil condition, and regeneration dynamics (Bugalho et al., 2011; Filazzola et al., 2020; Vaz et al., 2024), whereas low to moderate use may open niches and reduce competitive pressure (Kuiters & Slim, 2003; Pulido & Díaz, 2005; McEvoy et al., 2006; Schieltz & Rubenstein, 2016). In rotational systems, this interplay creates strong spatiotemporal heterogeneity in both grazing pressure and grazing history—features likely to influence seedling resprouting and survival but

seldom quantified jointly with multi-year management records and individual seedling fates (López-Sánchez et al., 2014).

Understanding context dependence also requires attending to proximate covariates that govern early performance. Seedling size (height) integrates reserves and rooting depth, predicting tolerance to damage and drought (Tyler et al., 2006; Clarke et al., 2013; Vaz et al., 2019). Shrubs can act as nurse cover or, conversely, intensify competition, with consequences for microsite moisture and protection from trampling (Pulido & Díaz, 2005; Díaz et al., 2021; Listopad et al., 2018). Finally, short-term climatic water balance modulates hydraulic stress during vulnerable stages, potentially tipping survival under otherwise similar grazing regimes (Díaz et al., 2021). Against this background, robust inference demands designs that couple long-run grazing information with individual-level fates and microhabitat/climate context in real paddocks.

Using a 12-year, paddock-level dataset on cattle grazing pressure under rotational grazing, together with individual survival monitoring of 8431 cork oak seedlings, we tested how cattle grazing alters cork oak regeneration—seedling survival and resprouting. First, we tested how seedling survival differs between ungrazed and grazed paddocks, predicting higher survival in the absence of cattle. Second, within grazed paddocks, we evaluated how grazing pressure (moderate vs. high) and grazing history (old vs. recent) affect survival, expecting lower survival under high pressure and under recent grazing. Because resprouting can promote persistence after top-kill, we further expected resprouting seedlings to survive longer than non-resprouters. Third, we examined whether cattle grazing reduces the probability that seedlings resprout and whether resprouting probability varies with grazing pressure and history, predicting lower resprouting under high pressure and recent grazing.

2. Materials and methods

2.1. Study area

The study was conducted between November 2021 and February 2023 in an 18000-ha cork oak woodland—known as *montado* (or *dehesa* in Spain)—in central Portugal. The area comprises grazed and ungrazed paddocks enclosed by barbed-wire fencing and is part of Companhia das Lezírias (CL; 38°50′ N, 8°49′ W), a multi-use, state-owned agrosilvopastoral estate and core site of the Long-Term Socio-Ecological Research platform Montado (www.ltsermontado.pt). Since the 19th century, CL has been managed for cork production, extensive cattle grazing, recreational hunting, and, more recently, biodiversity conservation. The region has a Mediterranean climate with hot, dry summers and mild, wet winters (Vaz et al., 2024). In 2022, annual precipitation was 502 mm, and the mean monthly temperature was 17.1 °C (min/max: 5.6–30.8 °C). The terrain is mostly flat (1–53 m elevation), with sandy, acidic soils (pH 5.4–6.3) low in organic matter and water retention, predominantly Podzols and hydromorphic types (Concostrina-Zubiri et al., 2017).

Cork oak trees at CL have a mean basal area of 13.0 m²/ha and an average density of 53.6 trees/ha (Mexia et al., 2022), with 24–49% canopy cover (Listopad et al., 2018). Most individuals are 4–14 m tall and 10–45 cm in diameter at breast height, DBH (Vaz et al., 2011). The most common understory species are *Ulex australis*, *Cistus salviifolius*, *Myrtus communis*, *Cistus crispus*, *Genista triacanthus*, and *Cistus ladanifer* (Carrilho et al., 2017), along with annual grasses and forbs such as *Tolpis barbata*, *Agrostis pourretii*, and *Ornithopus compressus* (Vaz et al., 2024). Cattle grazing is extensive and rotational, with herds of 50–300 head moved among padocks. Stocking rates range from 0.5 to 1.1 LSU ha^{-1}, typically lower in summer (Gonçalves et al., 2012).

2.2. Experimental design

We used 12 years of grazing records (2009–2021) to classify paddocks by grazing pressure and history. Grazing pressure was defined as moderate (≤150 LSU ha^{-1} days $year^{-1}$) or high (>150; Gonçalves et al., 2012; Arosa et al., 2017). Paddocks with consistently low grazing were excluded due to low replication. Grazing history was categorized as *recent* (cattle present during the two years prior to and typically during the study) or *old* (no cattle for two years before the study), though all the paddocks had cattle presence from 2009 to 2019.

To test the effects of grazing pressure and history on seedling survival, we selected 20 grazed paddocks—five per treatment combination: old–moderate, old–high, recent–moderate, and recent–high. For the grazed vs. ungrazed comparison, we selected four of these grazed paddocks (one per treatment) and matched them with four nearby ungrazed paddocks (>12 years without cattle) with similar habitat. All paddocks were ≥5 ha and separated by at least 400 m.

2.3. Data collection

In each paddock, we randomly selected three healthy adult cork oaks (10–45 cm DBH), spaced ≥100 m apart and ≥50 m from roads or paddock edges. Around each tree, a 20 m radius circular plot was established. All naturally established cork oak seedlings ≤15 cm tall were tagged with numbered plastic binder spines, and their positions recorded using polar coordinates—distance to the target tree (measured with a laser rangefinder, 1 mm precision) and azimuth angle (measured with a sighting compass from magnetic north).

Seedling survival was monitored seven times (Nov–Dec 2021; Jan–Feb, Mar, Jun–Jul, Aug, Sep 2022; Feb 2023), with census intervals adapted to field logistics and seasonal conditions. Only seedlings recorded at the first census were included; new recruits were negligible during

the sampling period and were excluded from analysis. Resprouting was noted as a binary variable (yes/no), defined as the reemergence of green tissue on individuals previously fully desiccated or with no visible aboveground biomass. Seedlings were considered dead if they failed to resprout within 384 days (Vaz et al., 2019), remained unchanged across consecutive censuses, or were found uprooted with tags attached or nearby.

Seedling height (main stem, in mm) was measured during the first, fourth, and final census. For seedlings that died earlier, the last recorded value was used. Microhabitat was characterized by the distance to the edge of the tree crown (not used in analyses, as nearly all seedlings were under canopy) and distance to the nearest shrub canopy edge (positive values indicating open ground).

To capture localized grazing intensity, cattle dung was counted around each tree at all seven censuses. For each seedling, we used the dung count from its corresponding tree at each census or the last recorded value if it died earlier.

To characterize recent climate, we calculated the Standardized Precipitation–Evapotranspiration Index (SPEI) at a 1-month scale using the *SPEI* v1.7 R package (Vicente-Serrano et al., 2010; Beguería & Vicente-Serrano, 2023). Monthly climate data from CL (Jan 2021–Feb 2023) included precipitation, minimum and maximum air temperature, and extraterrestrial radiation (Ra). Potential evapotranspiration (PET) was estimated using the Hargreaves method (Tmin, Tmax, Ra, latitude). Climatic water balance was computed as precipitation minus PET, and SPEI values preceding each census were included in survival models. Positive SPEI values indicate wet conditions; negative values, drought.

2.4. Statistical analysis

2.4.1. Seedling survival

To test whether seedling survival differed between grazed and ungrazed paddocks, we fitted a Bayesian mixed-effects survival model assuming a lognormal distribution. Survival time (days since first census) was modeled as interval-censored when death occurred between censuses and right-censored if the seedling was still alive at study end. Grazing treatment (grazed vs. ungrazed) was included as a fixed effect, and random intercepts accounted for seedlings nested within trees and trees within paddocks.

To assess effects of grazing pressure and history, we fitted a second lognormal Bayesian survival model with the same censoring structure. Fixed effects included grazing pressure (moderate vs. high), grazing history (old vs. recent), and their interaction. We added five covariates: seedling height, resprouting status (yes/no), distance to the nearest shrub, number of dung piles (proxy for localized grazing), and SPEI. All continuous predictors were centered and standardized; variance inflation factors were <2.1, indicating low multicollinearity (Lüdecke et al., 2021). For parsimony, we also fitted an additive model (without interaction) but leave-one-out cross-validation of expected log predictive density (ΔELPD LOO) favored the interaction model (ΔELPD LOO = −3.6 ± 2.5 SE; Vehtari et al., 2017). We further tested the removal of each covariate (excluding grazing variables) one at a time, interpreting ΔELPD LOO differences >2 × SE as meaningful (Vaz et al., 2021); results supported the full model.

Models were fitted using the *brms* package (Bürkner, 2017) in Stan (http://mc-stan.org/). Weakly informative priors were used to improve convergence while avoiding overfitting (Gelman et al., 2020): Normal(0, 3) for the fixed effect in the grazed vs. ungrazed model, and Normal(0, 5) and Normal(0, 1) for categorical and numeric predictors, respectively, in the

grazing pressure × history model. Each model was run with four MCMC chains (4000 iterations, 1000 warm-up), yielding 12000 post-warm-up samples. Convergence was assessed via trace plots and R□ (all ≤1.1). We also compared model distributions using leave-one-out cross-validation, with lognormal consistently outperforming Weibull and exponential alternatives (lower LOOIC). Posterior predictive checks confirmed model adequacy.

2.4.2. Resprouting probability

To assess whether grazing influenced seedling resprouting (yes/no), we fitted two Bayesian mixed-effects logistic regression models (Bernoulli, logit link). The first included grazing treatment (grazed vs. ungrazed) as a fixed effect, with a Normal(0, 4) prior. The second included grazing pressure and history, with Normal(0, 8) priors. Both models accounted for trees nested within paddocks in the random-effects structure. For the second model, we tested the interaction between grazing pressure and history but found no support for improved fit (ΔELPD LOO = −0.2 ± 0.5 SE), and thus retained the additive model. Diagnostics, convergence checks, and inference procedures followed those described above.

All analyses were conducted in R v.4.5.0 (R Core Team, 2024). Inference was based on posterior distributions and 95% credible intervals. Covariates whose posterior β intervals did not overlap zero were interpreted as having strong effects (McElreath, 2018).

3. Results

We monitored a total of 8431 cork oak seedlings across the 24 paddocks. By the end of the study period, 53% of the seedlings had survived (Table 1). Most seedlings (99%) remained under the canopy of adult cork oaks at the final census, while 15% were located beneath shrub cover. Survival was higher in the four ungrazed paddocks, where 62% of 1051 individuals persisted, compared to 51% survival among the 7380 seedlings in grazed

paddocks. Within grazed areas, 58% of 4628 seedlings survived in paddocks with older grazing history—where cattle had been absent during the last two years—compared to 39% of 2752 seedlings in paddocks with recent grazing activity. Under moderate grazing pressure, 52% of 5679 seedlings survived, compared to 49% of 1701 under high pressure. Among the 4441 seedlings that survived, 30% resprouted at least once during monitoring, whereas only 1% of the 3990 that ultimately died had ever resprouted before dying.

3.1. Survival: grazed vs. ungrazed paddocks

After accounting for random effects (trees nested within paddocks), our Bayesian mixed-effects lognormal survival model (Table 2) indicated that seedlings in the four ungrazed paddocks had higher survival than those in four nearby grazed paddocks with similar conditions. Nonlinear hypothesis testing (Bürkner, 2017; Clark, 2020; Vaz et al., 2021) showed strong support for this contrast: we estimate a 98% posterior probability that seedling survival was higher in the absence of cattle grazing. The model-predicted median survival time was 302 days (95% credible interval: 226–421) in grazed paddocks, compared to 493 days in ungrazed paddocks—a 63% increase (95% CI: 363–653), with the latter exceeding the study duration (Fig. 1).

3.2. Survival: grazing pressure and grazing history

The Bayesian survival model (Table 2) revealed that both grazing pressure and grazing history affected seedling longevity. Median predicted survival time was lower under high grazing pressure (256 days) than under moderate pressure (460 days; Fig. 2A). Similarly, seedlings in paddocks with recent grazing history had shorter predicted survival (199 days) than those with older grazing history (460 days; Fig. 2B). We found strong posterior support for these effects: there was a 97% probability that high grazing pressure reduced survival

compared to moderate pressure, and a 100% probability that recent grazing had a negative effect compared to older grazing.

Analysis of the interaction between grazing pressure and grazing history (Fig. 2C) showed that the effect of grazing history was more pronounced under moderate pressure than under high pressure. Under high grazing pressure, the 95% credible interval for the difference between recent and old grazing ranged from –571 to 1044 days, overlapping zero and suggesting weak evidence for a difference. Under moderate pressure, although the 95% credible interval (–334 to 1348 days) also included zero, 80% of posterior draws supported greater survival in the 'old' grazing condition (80% CI: –110 to 763 days).

Among the covariates, seedling height and resprouting status were positively associated with survival. The model predicts that a 15 cm seedling has a 58% longer lifespan than a 5 cm seedling (654 vs. 413 days). Resprouting had the strongest effect among all predictors, with resprouting seedlings reaching a predicted survival of 2351 days—more than five times that of non-resprouters (460 days; Fig. 2E). In contrast, distance from shrub cover had the weakest effect. Still, there was a 95% probability that seedlings located farther from shrubs had slightly lower survival. For example, seedlings located 5 m from a shrub had a 6% shorter predicted lifespan than those beneath shrub cover (436 vs. 466 days; Fig. 2F).

Two additional covariates—cattle dung abundance and SPEI—were positively associated with seedling survival. Increased dung counts, used as a proxy for very recent cattle presence, were linked to longer survival times, with model predictions indicating a twofold increase in survival between areas with 50 and 100 dung piles (Fig. 2G). Higher SPEI values, indicative of wetter recent conditions, were also associated with increased survival (Fig. 2H).

3.3. Resprout: grazed vs. ungrazed paddocks

Seedlings in ungrazed paddocks were more likely to resprout than those in grazed paddocks. According to our Bayesian mixed-effects logistic regression model (Table 3), the posterior probability of resprouting was 0.19 (95% CI: 0.13–0.26) in ungrazed paddocks, compared to 0.10 (0.05–0.17) in grazed paddocks (a 47% decrease; Fig. 3A). The model estimated a negative effect of grazing on resprouting, with 98% of posterior draws supporting a lower probability in grazed paddocks.

3.4. Resprout: grazing pressure and grazing history

Seedlings exposed to high grazing pressure were half as likely to resprout as those under moderate pressure (0.08 vs. 0.16; Fig. 3B). Although the 95% credible interval for the effect of grazing pressure overlapped zero (–2.32 to 0.58), 87% of posterior draws supported reduced resprouting under high grazing. In contrast, there was strong evidence for a negative effect of recent grazing history, with 99% of posterior draws supporting lower resprouting probability. Seedlings in recently grazed paddocks had a resprouting probability of 0.04, one quarter of that observed in paddocks with older grazing history (0.16; Fig. 3C).

4. Discussion

Our data provide field evidence on a long-standing question in Mediterranean woodlands: how cattle use shapes the fate of cork-oak seedlings—and, more broadly, of young trees establishing under recurrent disturbance. Leveraging 12 years of paddock-level grazing records and individual monitoring of 8431 seedlings—plus microhabitat and climatic balance data—we disentangle grazing intensity from recency and link them to both survival and resprouting capacity. Two results stand out. First, grazing depresses survival not only in aggregate (ungrazed > grazed) but also along management gradients: high pressure and

especially recent use shorten lifespans, whereas wetter recent conditions strongly enhanced survival. Second, resprouting is the dominant axis of persistence—seedlings that resprout live markedly longer—yet cattle reduce the probability of resprouting, with recent use exerting the sharpest penalty.

4.1. Grazing and resprout effects on seedling survival

Seedling survival was higher in ungrazed than in grazed paddocks, echoing patterns for Mediterranean oaks in Iberian agroforestry systems (Plieninger et al., 2010; Ritsche et al., 2021). The net negative signal of grazing accords with classic herbivory mechanisms—direct shoot consumption, repeated nipping and trampling, and soil compaction—plus shifts in soil structure and water infiltration that constrain root establishment (Pulido et al., 2010; Laskurain et al., 2013; Moradi et al., 2021; Palmerlee et al., 2025). Although grazing can suppress annual grasses and overall cover, potentially easing competition and sometimes reducing pressure from insects or small mammals (Tyler et al., 2008; Muñoz et al., 2009; Canelo et al., 2025; Vaz et al., 2024), these countervailing effects did not offset cattle impacts here.

Longevity declined with higher pressure and with more recent use: median survival fell from 460 to 256 days under high versus moderate pressure, and from 460 to 199 days in recently grazed versus ‘old’ (two-year hiatus) paddocks. These main effects fit herbivory theory—frequent defoliation and trampling reduce photosynthetic area, exhaust reserves, and delay ‘escape in size’ (Belsky et al., 1993; Rosenthal & Kotanen, 1994)—while compaction and litter removal depress moisture and organic matter, further limiting recovery (Pulido et al., 2010; Laskurain et al., 2013; Moradi et al., 2021). At paddock scale, intense or continuous use reduces safe sites and regeneration nuclei, narrowing the window for

persistence despite any competition release from grazed swards (Tyler et al., 2008; Muñoz et al., 2009; López-Sánchez et al., 2016; Perea et al., 2017).

The pressure × history interaction indicates that a two-year exclusion boosts survival only where background pressure was moderate. Under such conditions, release from cattle plausibly enables recovery of photosynthetic tissue, rebuilding of carbohydrate reserves, and root consolidation before renewed disturbance. Under high pressure, however, two years appear insufficient to reverse cumulative defoliation and compaction—an ecological legacy of heavily used pastures (Aronson et al., 2009; Pulido et al., 2010). Thus, regeneration is both intensity-dependent and temporally contingent: cohorts require moderate use plus extended rest to pass the most vulnerable stages.

Initial height strongly predicted persistence (a 15 cm seedling lived 58% longer than a 5 cm seedling), consistent with greater photosynthetic tissue, biomass, deeper roots, and reserves buffering stress and aiding recovery (Belsky et al., 1993; Rosenthal & Kotanen, 1994; Kobe et al., 1995; Tyler et al., 2006). Grazing suppresses height via browsing and trampling and indirectly through compaction and litter removal that reduce moisture and organic matter (Marcora et al., 2013; Laskurain et al., 2013; Moradi et al., 2021; Amsten et al., 2020). Because cattle target small, palatable shoots with limited structural or chemical defenses (Carmona et al., 2013; Göldel et al., 2016; Roula et al., 2019), intermittent escape in size can improve survival under continued use (Uytvanck et al., 2010).

Resprouting was the strongest predictor of survival. After top-kill, cork-oak seedlings can rebuild canopy area from root reserves and re-mobilization of non-structural carbohydrate (NSC) reserves, a classic plant tolerance pathway under recurrent herbivory (Belsky et al., 1993; Rosenthal & Kotanen, 1994; Fornoni, 2011; Clarke et al., 2013; Pausas et al., 2018; Smith et al., 2018; Resco de Dios et al., 2020). In *Quercus*, resprouting vigor scales with root

NSC pools and below-ground bud banks, supported by high root:shoot allocation and plastic hydraulic adjustments sustaining regrowth under drought (Clarke et al., 2013; Smith et al., 2018; Resco de Dios et al., 2020; Pausas et al., 2018). In cork oak, early taproot development and cotyledonary reserves fuel bud activation and shoot replacement, promoting persistence through summer droughts and after damage (Arosa et al., 2015; Zhang et al., 2019; Petersson et al., 2020). Seedlings that resprouted outlived non-resprouters by a wide margin, matching these mechanisms.

Shrub proximity conferred a modest advantage (~6% longer predicted lifespan beneath shrubs vs. 5 m away), consistent with nurse-plant effects that buffer heat and water stress, improve soil infiltration, and reduce trampling/browsing (Gómez-Aparicio et al., 2004; Smit et al., 2008; Plieninger et al., 2004; Pulido & Díaz, 2005; Díaz et al., 2021). In our system, *Ulex* spp. likely supplied shade, physical protection, and soil N inputs, favouring early cork oak seedling establishment. Other shrubs can act as competitors, however, so net effects depend on species identity and management. Because shrub clearing is routinely used to maintain open structure and reduce fire risk, the consequences for recruitment will differ if nurse shrubs are removed versus primarily competitive ones (Aronson et al., 2009; López-Sánchez et al., 2016). Prior work shows shrub cover can partially offset grazing impacts on oak seedlings (Pulido et al., 2010; Plieninger et al., 2011; Perea et al., 2016; Mochi et al., 2022); in our study this facilitation was detectable but small relative to the influences of grazing regime and resprouting.

Local dung abundance—a proxy for very recent cattle activity—was positively associated with survival. This likely reflects fine-scale heterogeneity in cattle use: animals concentrate in microsites with better shade, moisture, or forage that also favor seedlings (Ganskopp & Bohnert, 2009). Dung can locally enrich organic matter and nutrients, enhance water-holding capacity, and stimulate bioturbation (Huerta et al., 2018; Wang & Hou, 2022), sometimes

offering short-term protection from trampling/browsing (Ocumpaugh et al., 1996) and reducing desiccation risk (Leiva & Sobrino-Mengual, 2023). Such signatures can create microsites of higher survival within broadly negative grazing contexts.

Wetter recent conditions (higher 1-month SPEI) were also associated with longer survival, consistent with water-balance controls on Mediterranean recruitment: brief improvements in hydraulic status can lift persistence during vulnerable stages (Vicente-Serrano et al., 2010; Beguería & Vicente-Serrano, 2023). Although cork oak exhibits drought-coping traits—early taproot development and below-ground reserves (Costa et al., 2010; Mendes et al., 2016; Arosa et al., 2015)—recent climate still mattered. Thus, while grazing history, pressure, and resprouting dominated, short wet spells provided a consistent, positive nudge to longevity.

4.2 Grazing and probability of seedling resprout

Cattle reduced the likelihood that seedlings would resprout, with the strongest penalty under "recent" use. Mechanistically, successful resprouting after top-kill requires an intact bud bank at the root collar/lignotuber and sufficient below-ground carbohydrates to fuel rapid shoot replacement; frequent, recent defoliation and trampling damage basal meristems and draw down reserves, suppressing bud activation and sprout persistence—classic tolerance dynamics under recurrent disturbance (Belsky et al., 1993; Rosenthal & Kotanen, 1994; Fornoni, 2011; Clarke et al., 2013). Two proximate levers align with our pattern: (i) reserve status and stubble integrity—seedlings retaining cotyledons and adequate residual shoot tissue resprout more vigorously (Arosa et al., 2015; Zhang et al., 2019; Petersson et al., 2020); and (ii) hydraulic safety—brief rest periods can restore water status and permit reserve rebuilding, whereas late-season, repeated use pushes plants toward hydraulic failure, limiting sprout initiation (Clarke et al., 2013). Accordingly, a two-year release of grazing in "old"

paddocks likely allowed reserve recovery and bud maintenance, whereas “recent” grazing curtailed both processes, lowering resprouting odds.

5. Conclusions

Our study links a uniquely resolved grazing record to individual fates of 8431 seedlings and shows, unequivocally, that cattle use depresses cork-oak recruitment both in aggregate and along management gradients. Disentangling intensity from recency, we find that high pressure and recent use shorten lifespans, whereas wet periods (SPEI) measurably boost survival. Resprouting emerges as the dominant axis of persistence—seedlings that resprout live far longer—but cattle simultaneously suppress the probability of resprouting, with recent use exacting the sharpest penalty. Microsite context modulates these signals as well: shrubs confer small facilitative benefits and dung patches can mark locally favorable conditions, but neither offsets sustained grazing. Together, the results argue for adaptive rotational strategies that pair moderate stocking with multi-year rest periods long enough to rebuild bud banks and below-ground reserves; a two-year hiatus helps under moderate pressure but appears insufficient where pressure remains high. More broadly, our findings clarify when and why early life stages can persist in working Mediterranean woodlands, providing a mechanistic basis for reconciling production and regeneration in oak agroforestry.

CRediT authorship contribution statement

Abdullah Ibne Wadud: Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft. **João Craveiro**: Investigation, Writing – review & editing. **Simone Erroi**: Investigation, Writing – review & editing. **Sandra Alcobia**: Data curation, Writing – review & editing. **Miguel N Bugalho**: Supervision, Writing – review & editing. **Manuela Branco**: Conceptualization, Supervision, Writing – review & editing.

Pedro Gonçalves Vaz: Conceptualization, Supervision, Methodology, Resources, Formal analysis, Visualization, Writing – review & editing.

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Table 1. Number of cork oak seedlings that survived, resprouted, and died in each grazing treatment. Seedling survival was monitored within 24 paddocks distributed as shown. Within each paddock, survival was monitored around (20 m circles) 3 cork oak trees.

				survivals			deaths			total
grazing	grazing history	grazing pressure	no. of paddock	no resprout	resprout	subtotal	no resprout	resprout	subtotal	
grazed	old	moderate	5	1724	665	2389	1502	10	1512	3901
		high	5	142	174	316	410	1	411	727
		subtotal	*10*	*1866*	*839*	*2705*	*1912*	*11*	*1923*	*4628*
	recent	moderate	5	328	233	561	1204	13	1217	1778
		high	5	498	24	522	444	8	452	974
		subtotal	*10*	*826*	*257*	*1083*	*1648*	*21*	*1669*	*2752*
	subtotal		20	2692	1096	3788	3560	32	3592	7380
ungrazed			4	435	218	653	397	1	398	1051
		total	*24*	*3127*	*1314*	*4441*	*3957*	*33*	*3990*	*8431*

Table 2. Summary of the fixed effects from the mixed-effects Bayesian models evaluating the impact of cattle grazing on cork oak seedling survival. The top section presents results from a model comparing grazed and ungrazed paddocks, while the bottom section refers to grazed paddocks only and evaluates the effects of grazing pressure (moderate vs. high), grazing history (old vs. recent), and additional covariates. CI = 95% credible interval; β<>0 = posterior probability that the effect is greater (or smaller) than zero, depending on the sign of the estimate; Notable = asterisk indicates effects whose CI excludes zero (or lies very close to zero). The potential scale reduction factor (Rhat) was 1.00 for all parameters.

Model / Parameter	β	Error	2.5% CI	97.5% CI	β<>0	Notable
Grazed vs. ungrazed						
Intercept	6.20	0.15	5.89	6.48	1.00	*
Grazed (yes)	-0.48	0.22	-0.90	-0.05	0.98	*
Grazing pressure & history						
Intercept	5.89	0.23	5.45	6.38	1.00	*
Grazing pressure (high)	-0.59	0.32	-1.25	0.03	0.97	*
Grazing history (recent)	-0.85	0.33	-1.52	-0.25	1.00	*
Seedling height	0.15	0.01	0.13	0.17	1.00	*
Resprout (yes)	1.63	0.06	1.52	1.74	1.00	*
Distance to shrub	-0.02	0.01	-0.05	0.00	0.95	
No. of dung	0.44	0.04	0.37	0.51	1.00	*
SPEI	0.58	0.01	0.56	0.60	1.00	*
Grazing pressure (high) × Grazing history (recent)	1.22	0.45	0.35	2.15	1.00	*

Table 3. Summary of the fixed effects from the mixed-effects Bayesian logistic regression models evaluating the effects of cattle grazing on the probability of cork oak seedling resprouting. The top section compares grazed and ungrazed paddocks; the bottom section refers to grazed paddocks only, evaluating the effects of grazing pressure and grazing history. Model output structure and notation are as in Table 2.

Model / Parameter	β	Error	2.5% CI	97.5% CI	β<>0	Notable
Grazed vs. ungrazed						
Intercept	-1.44	0.25	-1.94	-0.97	1.00	*
Grazed (yes)	-0.78	0.39	-1.60	-0.05	0.98	*
Grazing pressure & history						
Intercept	-1.63	0.61	-2.83	-0.40	0.99	*
Grazing pressure (high)	-0.79	0.73	-2.32	0.58	0.87	
Grazing history (recent)	-1.56	0.71	-3.03	-0.20	0.99	*

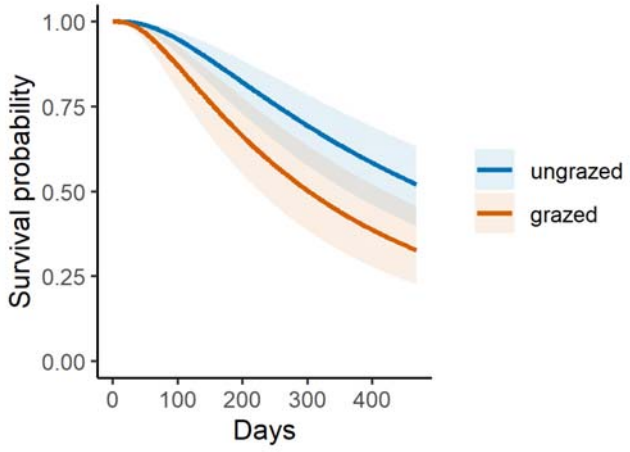

Figure 1. Fitted survival curves (± 95% credible intervals) for cork oak seedlings in ungrazed and cattle-grazed paddocks over the duration of the study, estimated using a Bayesian mixed-effects lognormal survival model.

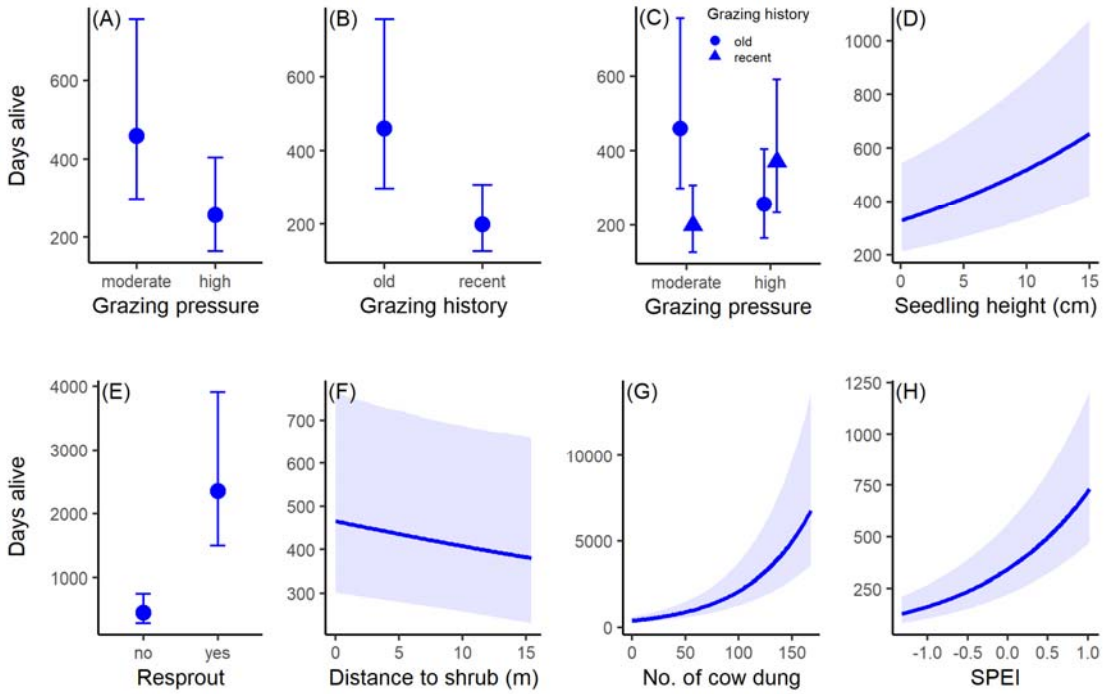

Figure 2. Model-fitted survival times for cork oak seedlings as a function of grazing treatments and covariates, based on the Bayesian mixed-effects lognormal survival model. Panels show effects of grazing pressure, grazing history, their interaction, and additional covariates. Points or lines represent posterior medians; shaded areas and vertical bars indicate 95% credible intervals. See main text for panel descriptions.

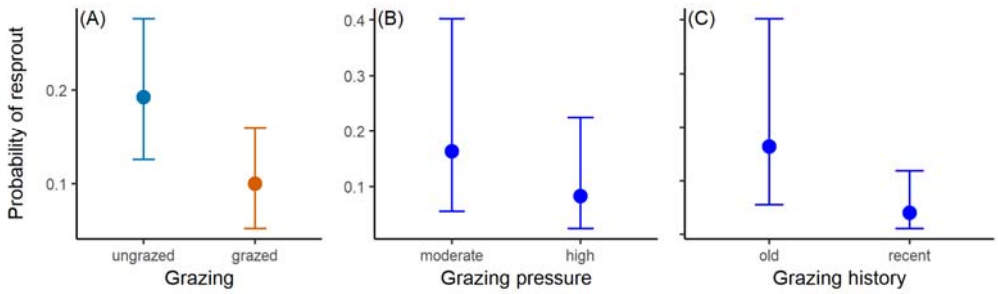

Figure 3. Model-fitted probability of resprouting in cork oak seedlings (posterior median ± 95% credible intervals) in response to grazing treatments, based on Bayesian mixed-effects logistic regression models. See main text for panel descriptions.