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

Authors: Abdullah Ibne Wadud[1], João Craveiro[1,2], Simone Erroi[1], Sandra Alcobia[3], Manuela Branco[4], Miguel N. Bugalho[1], Pedro Gonçalves Vaz[2].

[1] Centre for Applied Ecology "Prof. Baeta Neves" (CEABN-InBIO), School of Agriculture, University of Lisbon, Tapada da Ajuda, 1349-017, Lisbon, Portugal

[2] CE3C - Centre for Ecology, Evolution and Environmental Changes, CHANGE – Global Change and Sustainability Institute, Faculty of Science, University of Lisbon, Edificio C2, 5o andar, sala C2.5.37, Campo Grande, 1749-016 Lisbon, Portugal

[3] Technical Management Framework, Department of Forestry, Sustainability, and Biodiversity; Companhia das Lezírias, S.A., Largo 25 de abril, nº17, 2135-318 Samora Correia, Portugal

[4] Forest Research Centre (CEF), School of Agriculture, University of Lisbon, Tapada da Ajuda, 1349-017, Lisbon, Portugal

Correspondence: pjvaz@fc.ul.pt

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·ha^{-1}·days·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.

Acknowledgements

AIW (PT/BD/143139/2018) was funded by the Portuguese Science and Technology Foundation (FCT) through SUSFOR—Sustainable Forests and Products Doctoral Program (PD.00157.2012) and institutional supported by CEABN-InBIO UIDB/50027/2025; InBIO DOI 10.54499/LA/P/0048/2020). JC and PGV were funded by FCT through CE3C (UID/00329/2025) and CHANGE (DOI 10.54499/LA/P/0121/2020). PGV received funding from the AdaptForGrazing project (PRR-C05-i03-I-000035-LA4.3/4.4/4.6/4.7), supported by the EU (RRF) via IFAP (PRR).

References

Allen, V. G., Batello, C., Berretta, E. J., Hodgson, J., Kothmann, M., Li, X., McIvor, J., Milne, J., Morris, C., Peeters, A., & Sanderson, M. (2011). An international terminology for grazing lands and grazing animals. *Grass and Forage Science*, **66**, 2–28. https://doi.org/10.1111/j.1365-2494.2010.00780.x

Amsten, K., Cromsigt, J. P. G. M., Kuijper, D. P. J., Loberg, J. M., Churski, M., & Niklasson, M. (2021). Fire- and herbivory- driven consumer control in a savanna-like temperate wood-pasture: An experimental approach. *Journal of Ecology*, **109**, 4103–4114. https://doi.org/10.1111/1365-2745.13783

Aronson, J., Pereira, J. S., & Pausas, J. G. (2009). Natural Regeneration. In: Pausas, J. G., Maranon, T., Caldeira, M., Pons, J. (Eds.). Cork Oak Woodlands on the Edge: Ecology Adaptive Management and Restoration. Society for Ecological Restoration International.

Island Press, Washington, D.C., USA, pp. 114–126. ISBN 978-1-59726-479-2.

https://doi.org/10.1111/j.1526-100X.2010.00701.x

Arosa, M. L., Bastos, R., Cabral, J. A., Freitas, H., Costa, S. R., & Santos, M. (2017). Long-

term sustainability of cork oak agro-forests in the Iberian Peninsula: A model-based

approach aimed at supporting the best management options for the montado conservation.

Ecological modelling, **343**, 68–79. http://dx.doi.org/10.1016/j.ecolmodel.2016.10.008

Arosa, M. L., Ceia, R. S., Costa, S. R., & Freitas, H. (2015). Factors affecting cork oak

(*Quercus suber*) regeneration: acorn sowing success and seedling survival under field

conditions. *Plant Ecology & Diversity*, **8**, 519–528.

https://doi.org/10.1080/17550874.2015.1051154

Beguería, S., & Vicente-Serrano, S. M. (2023). SPEI: Calculation of the Standardized

Precipitation-Evapotranspiration Index. R package version 1.8.1.

https://doi.org/10.32614/CRAN.package.SPEI

Belsky, A. J., Carson, W. P., & Jensen, C. L. (1993). Overcompensation by plants: Herbivore

optimization or red herring? *Evolution Ecology*, **7**, 109–121.

https://doi.org/10.1007/BF01237737

Bond, W. J., & Midgley, J. J. (2001). Ecology of sprouting in woody plants: the persistence

niche. *Trends in Ecology & Evolution*, **16**, 45–51.

https://doi.org/https://doi.org/10.1016/S0169-5347(00)02033-4

Branco, M., & Ramos, P. A. (2009). Coping with pest and diseases. In J. Aronson, J. S.

Pereira, & J. G. Pausas (Eds.), *Cork oak woodlands on the edge* (pp. 103–112).

ISLANDPRESS

Brasier, C. M. (1992). Oak tree mortality in Iberia. *Nature*, **360**, 539–539.

Brooks, S., Gelman, A., Jones, G., & Meng, X.-L. (Eds.) (2011). *Handbook of Markov Chain Monte Carlo*. Chapman and Hall/CRC. https://doi.org/10.1201/b10905

Bugalho, M., Lecomte, X., Gonçalves, M., Caldeira, M. C., & Branco, M. (2011). Establishing grazing and grazing-excluded patches increases plant and invertebrate diversity in a Mediterranean oak woodland. *Forest Ecology and Management*, **261**, 2133–2139. https://doi.org/10.1016/j.foreco.2011.03.009.

Bürkner, P. C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, **80**, 1–28. https://doi.org/10.18637/jss.v080.i01

Canelo, T., Bogdziewicz, M., Pérez- Izquierdo, C., Gaytán, A., & Bonal, R. (2025). Livestock as a biological pest control: Experimental validation for oak savannas. *Journal of Applied Ecology*, 62, 824–833. https://doi.org/10.1111/1365-2664.70012

Carmona, P. C., Azcárate, F. M., Oteros-Rozas, E., González, J. A., & Peco, B. (2013). Assessing the effects of seasonal grazing on holm oak regeneration: Implications for the conservation of Mediterranean dehesas. *Biological Conservation*, **159**, 240–247. http://dx.doi.org/10.1016/j.biocon.2012.11.015

Carrilho, M., Teixeira, D., Santos-Reis, M., & Rosalino, L. M. (2017). Small mammal abundance in Mediterranean Eucalyptus plantations: How shrub cover can really make a difference. *Forest Ecology and Management*, **391**, 256–263. https://doi.org/10.1016/j.foreco.2017.01.032

Catry, F., Rego, F., Moreira, F., Fernandes, P., & Pausas, J. (2010). Post-fire tree mortality in mixed forests of central Portugal. *Forest Ecology and Management*, **260**, 1184-1192. https://doi.org/10.1016/j.foreco.2010.07.010

Cierjacks, A., & Hensen, I. (2004). Variation of stand structure and regeneration of

    Mediterranean holm oak along a grazing intensity gradient. *Plant Ecology*, **173**, 215–223.

    https://doi.org/10.1023/B:VEGE.0000029322.75004.ad

Clark, M. (2020). lazerhawk: Miscellaneous functions mostly inspired by synthwave. R

    package version 0.2.4. https://github.com/m-clark/lazerhawk

Clarke, P. J., Lawes, M. J., Midgley, J. J., Lamont, B. B., Ojeda, F., Burrows, G. E., Enright,

    N. J., & Knox, K. J. E. (2013). Resprouting as a key functional trait: how buds, protection

    and resources drive persistence after fire. *New Phytologist*, **197**, 19–35.

    https://doi.org/https://doi.org/10.1111/nph.12001

Concostrina-Zubiri, L., Molla, L., Velizarova, E., & Branquinho, C. (2017). Grazing or not

    grazing: Implications for ecosystem services provided by biocrusts in Mediterranean cork

    oak woodlands. *Land Degradation & Development*, **28**, 1345–1353.

    https://doi.org/10.1002/ldr.2573

Costa, A., Pereira, H., & Madeira, M. (2010). Analysis of spatial patterns of oakdecline in

    cork oak woodlands in Mediterranean conditions. *Annals of Forest Science*, **67**, 204.

    https://dx.doi.org/10.1051/forest/2009097

Cruz, A., Pérez, B., Quintana, J. R., & Moreno, J. M. (2002). Resprouting in the

    Mediterranean-type shrub Erica australis affected by soil resource availability. *Journal of*

    Vegetation Science, **13**, 641–650. https://doi.org/10.1111/j.1654-1103.2002.tb02092.x

Dias, S. F., Miller, D. M., Marques, T. A., Marcelino, J., Caldeira, M. C., Cerdeira, J. O., &

    Bugalho, M. N. (2016). Conservation zones promote oak regeneration and shrub diversity in

    certified Mediterranean oak woodlands. *Biological Conservation*, **195**, 226–234.

    http://dx.doi.org/10.1016/j.biocon.2016.01.009.

Díaz, M., Sanchez-Mejía, T., & Moran-López, T. (2021). Long-term tree regeneration of fragmented agroforestry systems under varying climatic conditions. *Frontiers in Ecology and Evolution*, **9**. https://doi.org/10.3389/fevo.2021.640143.

FAO (2022). Grazing with trees – A silvopastoral approach to managing and restoring trees. *FAO Forestry Paper*, No. 187. Rome. https://doi.org/10.4060/cc2280en.

Filazzola, A., Brown, C., Dettlaff, M. A., Batbaatar, A., Grenke, J., Bao, T., Heida, I. P., & Cahill Jr, J. F. (2020). The effects of livestock grazing on biodiversity are multitrophic: a meta-analysis. *Ecology Letters*, **23**, 1298–1309. https://doi.org/10.1111/ele.13527.

Fornoni, J. (2011). Ecological and evolutionary implications of plant tolerance to herbivory. *Functional Ecology*, **25**, 399–407.

Ganskopp, D. C., & Bohnert, D. W. (2009). Landscape nutritional patterns and cattle distribution in rangeland pastures. *Applied Animal Behaviour Science*, **116**, 110–119. https://doi.org/10.1016/j.applanim.2008.10.006

Göldel, B., Araujo, A. C., Kissling, W. D., & Svenning, J. (2016). Impacts of large herbivores on spinescence and abundance of palms in the Pantanal, Brazil. *Botanical Journal of the Linnean Society*, **182**, 465–479. https://doi.org/10.1111/boj.12420

Gómez-Aparicio, L., Zamora, R., Gómez, J. M., Hódar, J. A., Castro, J., & Baraza, E. (2004). Applying plant facilitation to forest restoration in Mediterranean ecosystems: a meta-analysis of the use of shrubs as nurse plants. *Ecological Applications*, **14**, 1128–1138. https://doi.org/10.1890/03-5084

Gonçalves, P., Alcobia, S., Simões, L., & Santos-Reis, M. (2012). Effects of management options on mammal richness in a Mediterranean agro-silvo-pastoral system. *Agroforestry Systems*, **85**, 383–395. https://doi.org/10.1007/s10457-011-9439-7

Guimarães, M. H., Pinto-Correia, T., Costa Freitas, M. B., Ferraz-de-Oliveira, I, Sales-
Baptista, E., Ferragolo-da-Veiga, J. F., Marques, J. T., Pinto-Cruz, C., Godinho, C., & Belo,
A. D. F. (2023). Farming for nature in the Montado: the application of ecosystem services
in a results-based model. *Ecosystem Services*, **61**, 101524.
https://doi.org/10.1016/j.ecoser.2023.101524.

Harper, J. L. (1977). Population biology of plants. Academic Press, London.

Huaranca, J. C., Novaro, A. J., & Valdivia, C. E. (2022). Effects of livestock grazing on
biodiversity: A meta-analysis on three trophic levels. *Journal for Nature Conservation*, **66**,
126126. https://doi.org/10.1016/j.jnc.2021.126126.

Huerta, C., Arellano, L., & Cruz, M. (2018). Dung beetles (Coleoptera: Scarabaeidae,
Scarabaeinae) and dung removal in Mexican livestock pastures. *Revista Mexicana de
Biodiversidad*, **89**, 1280–1292. https://doi.org/10.22201/ib.20078706e.2018.4.2495

Jhwueng, D., Huzurbazar, S., O'Meara, B., & Liu, L. (2014). Investigating the performance
of AIC in selecting phylogenetic models. *Statistical Applications in Genetics and Molecular
Biology*, **13**, 459–475. https://doi.org/10.1515/sagmb-2013-0048

Kobe, R. K., Pacala, S. W., Silander, J. A., & Canham, C. D. (1995). Juvenile tree
survivorship as a component of shade tolerance. *Ecological Applications*, **5**, 517–532.
https://doi.org/10.2307/1942040

Kuiters, T. A., & Slim, A. P. (2003). Tree colonisation of abandoned arable land after 27
years of horse-grazing: the role of bramble as a facilitator of oak wood regeneration. *Forest
Ecology and Management*, **181**, 239–251. https//doi.org/10.1016/S0378-1127(03)00136-1.

LaMalfa, E. M., Kimuyu, D. M., Sensenig, R. L., Young, T. P., Riginos, C., & Veblen, K. E.
(2019). Tree resprout dynamics following fire depend on herbivory by wild ungulate
herbivores. *Journal of Ecology*, **107**, 2493–2502. https//doi.org/10.1111/1365-2745.13186

Laskurain, N. A., Aldezabal, A., Olano, J. M., Loidi, J., & Escudero, A. (2013). Intensification of domestic ungulate grazing delays secondary forest succession: evidence from exclosure plots. *Journal of Vegetation Science*, **24**, 320–331. https://doi.org/10.1111/j.1654-1103.2012.01469.x.

Leiva, M. J., & Sobrino-Mengual, G. (2023). Cattle dung and bioturbation by dung beetles improve oak seedling establishment in Mediterranean silvopastoral ecosystems. *New Forests*, **54**, 289–309. https://doi.org/10.1007/s11056-022-09922-0

Listopad, C., Köbel, M., Príncipe, A., Gonçalves, P., & Branquinho, C. (2018). The effect of grazing exclusion over time on structure, biodiversity, and regeneration of high nature value farmland ecosystems in Europe. *Science of the Total Environment*, **262**, 561–570. https://doi.org/10.1016/j.scitotenv.2017.08.018

López-Sánchez, A., Peláez, M., Dirzo, R., Fernandes, G. W., Seminatore, M., & Perea, R. (2019). Spatio-temporal variation of biotic and abiotic stress agents determines seedling survival in assisted oak regeneration. *Journal of Applied Ecology*, **56**, 2663–2674. https://doi.org/10.1111/1365-2664.13500.

López-Sánchez, A., Perea, R., Dirzo, R., & Roig, S. (2016). Livestock vs. wild ungulate management in the conservation of Mediterranean dehesas: Implications for oak regeneration. *Forest Ecology and Management*, **362**, 99–106. https://doi.org/10.1016/j.foreco.2015.12.002.

López-Sánchez, A., Schroeder, J., Roig, S., Sobral, M., & Dirzo, R., 2014. Effects of cattle management on oak regeneration in Northern Californian Mediterranean oak woodlands. *PLoS ONE*, **9**, e105472. https://doi:10.1371/journal.pone.0105472

Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P., & Makowski, D. (2021).

performance: An R package for assessment, comparison and testing of statistical models.

Journal of Open Source Software, **6**, 3139. https://doi.org/10.21105/joss.03139

Marcora, P. I., Renison, D., País-Bosch, A. I., Cabido, M. R., & Tecco, R. A. (2013). The

effect of altitude and grazing on seedling establishment of woody species in central

Argentina. *Forest Ecology and Management*, **291**, 300–307.

http://dx.doi.org/10.1016/j.foreco.2012.11.030

McCreary, D., Tietje, B., Davy, J., Larsen, R., Doran, M., Flavell, D., & Garcia, S. (2011).

Tree shelters and weed control enhance growth and survival of natural blue oak seedlings.

California Agriculture, **65**, 192–196. http://dx.doi.org/10.3733/ca.v065n04p192

McElreath, R. (2018). *Statistical rethinking: A Bayesian course with examples in R and Stan*.

2nd edn. Chapman & Hall/CRC.

McEvoy, M. P., McAdam, J. S., Mosquera-Losada, M. R., & Rigueiro-Rodríguez, A. (2006).

Tree regeneration and sapling damage of pedunculate oak *Quercus robur* in a grazed forest

in Galicia, NW Spain: a comparison of continuous and rotational grazing systems.

Agroforestry Systems, **66**, 85–92. https://doi.org/10.1007/s10457-005-2916-0

McKee, T. B., Doesken, N. J., & Kleist, J. (1993). The relationship of drought frequency and

duration to time scales. In: *Proceedings of the 8th Conference on Applied Climatology*, 12–

17 January, Anaheim, California. American Meteorological Society.

Mechergui, T., Pardos, M., Boussaidi, N., Jacobs, D. F., & Catry, F.X. (2023). Problems and

solutions to cork oak (*Quercus suber* L.) regeneration: a review. *iForest - Biogeosciences

and Forestry*, **16**, 10–22. https://doi.org/10.103832/ifor3945015

Mendes, M. P., Ribeiro, L., David, T. S., & Costa, A. (2016). How dependent are cork oak

(*Quercus suber* L.) woodlands on groundwater? A case study in southwestern Portugal.

Forest Ecology and Management, **378**, 122–130.

https://dx.doi.org/10.1016/j.foreco.2016.07.024

Mexia, T., Lecomte, X., Caldeira, M. C., & Bugalho, M. N. (2022). Conservation zones

increase habitat heterogeneity of certified Mediterranean oak woodlands. *Forest Ecology*

and Management, **504**, 119811. https://doi.org/10.1016/j.foreco.2021.119811

Milios, E., Pipinis, E. E., Kitikidou K., Batziou, M., Chatzakis, S., & Akritidou, S. (2014).

Are sprouts the dominant form of regeneration in a lowland *Quercus pubescens–Quercus*

frainetto remnant forest in Northeastern Greece? A regeneration analysis in the context of

grazing. *New Forests*, **45**, 165–177. http://dx.doi.org/10.1007/s11056-013-9399-z.

Mochi, L. S., Mazía, N., Biganzoli, F., & Aguiar, M. R. (2022). Contrasting effects of

grazing on the early stages of woody encroachment in a Neotropical savanna. *Basic and*

Applied Ecology, **60**, 13–24. https://doi.org/10.1016/j.baae.2022.01.007

Monfort-Bague, I. P., Vega-García, C., Jürguens, J., Teixidó, A., & Casals, P. (2020). Stem

selection reduces the resprouting vigor of box-tree (*Buxus sempervirens* L.) understory in

sub-Mediterranean pine forest. *European Journal of Forest Research*, **139**, 947–958.

https://doi.org/10.1007/s10342-020-01297-1

Moradi, M., Jorfi, M. R., Basiri, R., Naanaei, S. U., & Heydari, M. (2021). Beneficial effects

of livestock exclusion on tree regeneration, understory plant diversity, and soil properties in

semiarid forests in Iran. *Land Degradation & Development*, **33**, 324–332.

https://doi.org/10.1002/ldr.4154

Moreira, F., Viedma, O., Arianoutsou, M., Curt, T., Koutsias, N., Rigolot, E., Barbati, A., Corona, P., Vaz, P., Xanthopoulos, G., Mouillot, F., & Bilgili, E. (2011). Landscape - wildfire interactions in southern Europe: implications for landscape management. *Journal of Environmental Management*, **92**, 2389–2402. https://doi.org/10.1016/j.jenvman.2011.06.028.

Muñoz, A., Bonal, R., & Díaz, M. (2009). Ungulates, rodents, shrubs: interactions in a diverse Mediterranean ecosystem. *Basic and Applied Ecology*, **10**, 151–160. https://doi.org/10.1016/j.baae.2008.01.003

Ocumpaugh, W. R., Archer, S., & Stuth, J. W. (1996). Switchgrass recruitment from broadcast seed vs. seed fed to cattle. *Journal of Range Management*, **49**, 368–371. https://doi.org/10.2307/4002599

Palmerlee, A., Vaughn, K., & Young, T. (2025). Escaping the browse trap : Patterns of natural blue oak regeneration in grazed landscapes. *Rangeland Ecology & Management*, **98**, 561–567. https://doi.org/10.1016/j.rama.2024.11.005

Paracchini, M. L., Petersen, J. E., Hoogeveen, Y., Bamps, C., Burfield, I., & van Swaay, C., (2008). High Nature Value Farmland in Europe. An estimate of the distribution patterns on the basis of land cover and biodiversity data. Office for Official Publications of the European Communities, Luxemburg.

Parsons, J., Motta, C., Sehgal, G., Miller-ter-Kuile, A., Young, H., & Orr, D. (2021). Interactive effects of large herbivores and climate on California oak seedling outcomes. *Forest Ecology and Management*, **502**, 119650. https://doi.org/10.1016/j.foreco.2021.119650

Pausas, J. G., Ribeiro, E., Dias, S. G., Pons, J., & Beseler, C. (2006). Regeneration of a

marginal *Quercus suber* forest in the eastern Iberian Peninsula. *Journal of Vegetation Science*, **17**, 729–738. https://doi.org/10.1111/j.1654-1103.2006.tb02496.x

Pausas, J. G., Lamont, B. B., Paula, S., Appezzato-da-Glória, B., & Fidelis, A. (2018).

Unearthing belowground bud banks in fire-prone ecosystems. *New Phytologist*, **217**, 1435–1448. https://doi.org/10.1111/nph.14982

Peláez, M., López-Sánchez, A., Fernandes G. W., Dirzo, R., Rodríguez-Calcerrada, J., &

Perea, R. (2025). Responses of oak seedlings to increased herbivory and drought: a possible trade-off? *Annals of Botany*, **135**, 341–356. https://doi.org/10.1093/aob/mcae178

Perea, R., López-Sánchez, A., & Dirzo, R. (2017). Differential tree recruitment in California

oak savannas: Are evergreen oaks replacing deciduous oaks? *Forest Ecology and Management*, **399**, 1–8. https://dx.doi.org/10.1016/j.foreco.2017.05.018

Perea, R., López-Sánchez, A., & Roig, S. (2016). The use of shrub cover to preserve

Mediterranean oak dehesas: a comparison between sheep, cattle and wild ungulate management. *Applied Vegetation Science*, **19**, 244–253. https://dx.doi.org/10.1111/avsc.12208

Petersson, L. K., Löf, M., Jensen, A. M., Chastain, D. R., & Gardiner, E. S. (2020). Sprouts

of shoot-clipped oak (*Quercus alba* and *Q. robur*) germinants show morphological and photosynthetic acclimation to contrasting light environments. *New Forests*, **51**, 817–834. https://doi.org/10.1007/s11056-019-09762-5

Pinto-Correia, T., Ribeiro, N., & Sá-Sousa, P. (2011). Introducing the montado, the cork and

holm oak agroforestry system of Southern Portugal. *Agroforestry Systems*, **82**, 99–104. http//doi.org/10.1007/s10457-011-9388-1.

Plieninger, T., Hartel, T., Martín-López, B., Beaufoy, G., Bergmeier, E., Kirby, K., Montero, M. J., Moreno, G., Oteros-Rozas, E., & Van Uytvanck, J. (2015). Wood-pastures of Europe: Geographic coverage, social-ecological values, conservation management, and policy implications. *Biological Conservation*, **190**, 70–79. https://doi.org/10.1016/j.biocon.2015.05.014.

Plieninger, T., Pulido, F. J., & Konold, W. (2003). Effects of land-use history on size structure of holm oak stands in Spanish dehesas: implications for conservation and restoration. *Environmental Conservation*, **30**, 61–70. https://10.1017/s0376892903000055.

Plieninger, T., Pulido, F. J., & Schaich, H. (2004). Effects of land-use and landscape structure on holm oak recruitment and regeneration at farm level in *Quercus ilex* L. dehesas. *Journal of Arid Environment*, **57**, 345–364. https://doi.org/10.1016/S0140-1963(03)00103-4

Plieninger, T., Rolo, V., & Moreno, G. (2010). Large-scale patterns of *Quercus ilex*, *Quercus suber,* and *Quercus pyrenaica* regeneration in Central-Western Spain. *Ecosystems*, **13**, 644–660. https://doi.org/10.1007/s10021-010-9345-2

Plieninger, T., Schaich, H., & Kizo, T. (2011). Land-use legacies in the forest structure of silvopastoral oak woodlands in the Eastern Mediterranean. *Regional Environmental Change*, **11**, 603–615. https://doi.org/10.1007/s10113-010-0192-7.

Pulido, F., García, E., Obrador, J. J., & Moreno, G. (2010). Multiple pathways for tree regeneration in anthropogenic savannas: incorporating biotic and abiotic drivers into management schemes. *Journal of Applied Ecology*, **47**, 1272–1281. https://doi.org/10.1111/j.1365-2664.2010.01865.x

Pulido, F. J., & Díaz, M. (2005). Regeneration of a Mediterranean oak: A whole-cycle approach. *Écoscience*, **12**, 92–102. https://doi.org/10.2980/i1195-6860-12-1-92.1

R Core Team (2024). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Version 4.5.0. https://www.R-project.org/

Resco de Dios, V., Arteaga, C., Peguero-Pina, J. J., Sancho-Knapik, D., Qin, H., Zveushe, O. K., Sun, W., Williams, D. G., Boer, M. M., Voltas, J., Moreno, J. M., Tissue, D. T., & Gil-Pelegrín, E. (2020). Hydraulic and photosynthetic limitations prevail over root non-structural carbohydrate reserves as drivers of resprouting in two Mediterranean oaks. *Plant Cell and Environment*, **43**, 157–168. https://doi.org/10.1111/pce.13781

Ritsche, J., Katzensteiner, K., & Acácio, V. (2021). Tree regeneration patterns in cork oak landscapes of Southern Portugal: The importance of land cover type, stand characteristics and site conditions. *Forest Ecology and Management*, **486**, 118970. https://doi.org/10.1016/j.foreco.2021.118970

Rosenthal, J. P., & Kotanen, P. M. (1994). Terrestrial plant tolerance to herbivory. *Trends in Ecology and Evolution*, **9**, 145–148. https://doi.org/10.1016/0169-5347(94)90180-5

Roula, S. E., Bouhraoua, R. T., & Catry, F. X. (2019). Factors affecting post-fire regeneration after coppicing of cork oak (*Quercus suber*) trees in northeastern Algeria. *Canadian Journal for Forest Research*, **50**, 371–379. https://doi.org/10.1139/cjfr-2019-0181

Santos-Heredia, C., Andresen, E., & Zárate, D. A. (2010). Secondary seed dispersal by dung beetles in a Colombian rain forest: effects of dung type and defecation pattern on seed fate. *Journal of Tropical Ecology*, **26**, 355–364. https://doi.org/10.1017/S0266467410000192

Schieltz, J. M., & Rubenstein, D. I. (2016). Evidence based review: positive versus negative effects of livestock grazing on wildlife. What do we really know? *Environmental Research Letters*, **11**, 113003. https://doi.org/10.1088/1748-9326/11/11/113003.

Scott, E. R., Uriarte, M., & Bruna, E. M. (2021). Delayed effects of climate on vital rates lead to demographic divergence in Amazonian forest fragments. *Global Change Biology*, **28**, 463–479. https://doi.org/10.1111/gcb.15900

Smit, C., Ouden, J., & Díaz, M. (2008). Facilitation of *Quercus ilex* recruitment by shrubs in Mediterranean open woodlands. *Journal of Vegetation Science*, **19**, 193–200. https://doi.org/10.3170/2007-8-18352

Smith, M. G., Arndt, S. K., Miller, R. E., & Bennett, L. T. (2018). Trees use more non-structural carbohydrate reserves during epicormic than basal resprouting. *Tree Physiology*, **38**, 179–188. https://doi.org/10.1093/treephys/tpy099

Tyler, C. M., Davis, F. W., & Mahall, B. E. (2008). The relative importance of factors affecting age-specific seedling survival of two co-occurring oak species in southern California. *Forest Ecology and Management*, **255**, 3063–3074. https://doi.org/10.1016/j.foreco.2008.01.073.

Tyler, C. M., Kuhn, B., & Davis, F. W. (2006). Demography and recruitment limitations of three oak species in California. *The Quarterly Review of Biology*, **81**, 127–152. https://doi.org/10.1086/506025.

Uytvanck, J. V., Milotic, T., & Hoffmann, M. (2010). Interaction between large herbivore activities, vegetation, structure, and flooding affects tree seedling emergence. *Plant Ecology*, **206**, 173–184. https://doi.org/10.1007/s11258-009-9632-1

Vaz, P. G., Bugalho, M. N., & Fedriani, J. M. (2024). Grazing hinders seed dispersal during crop failure in a declining oak woodland. *Science of the Total Environment*, **907**, 167835. https://doi.org/10.1016/j.scitotenv.2023.167835

Vaz, P. G., Bugalho, M. N., Fedriani, J. M., Branco, M., Lecomte, X., Nogueira, C. & Caldeira, M. C. (2019). Unravelling associations between tree-seedling performance, herbivory, competition, and facilitation in high nature value farmlands. *Journal of Environmental Management*, **232**, 1066–1074. https://doi.org/10.1016/j.jenvman.2018.11.082

Vaz, P. G., Merten, E. C., Robinson, C. T., & Pinto, P. (2021). Severely burned wood from wildfires has low functional potential in streams. *Journal of Applied Ecology*, **58**, 1346–1356. https://doi.org/10.1111/1365-2664.13872

Vaz, P. G., Warren, D. R., Merten, E. C., Robinson, C., Pinto, P., & Rego, F. C. (2013). Effects of forest type and stream size on volume and distribution of stream wood: legacies of wildfire in a Euro-Mediterranean context. *Freshwater Science*, **32**, 126–141. https://doi.org/10.1899/12-091.1.

Vaz, P. G., Warren, D. R., Pinto, P., Merten, E. C., Robinson, C. T., & Rego, F. C. (2011). Tree type and forest management effects on the structure of stream wood following wildfires. *Forest Ecology and Management*, **262**, 561–570. https://doi.org/10.1016/j.foreco.2011.04.026

Vehtari, A., Gelman, A., & Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing*, **27**, 1413–1432. https://doi.org/10.1007/s11222-016-9696-4

Vicente-Serrano, S. M., Beguería, S., & López-Moreno, J. I. (2010). A multiscalar drought index sensitive to global warming: The Standardized Precipitation Evapotranspiration Index. *Journal of Climate*, **23**, 1696–1718. https://doi.org/10.1175/2009JCLI2909.1

Wadud, A. I., Bugalho, M. N., & Vaz, P. G. (2024). Meta-analysis of livestock effects on tree regeneration in oak agroforestry systems. *Journal of Environmental Management*, **364**, 121498. https://doi.org/10.1016/j.jenvman.2024.121498

Wang, S., & Hou, F. (2023) Higher dung seedling density increases livestock dung greenhouse gas emissions in an alpine meadow. *Journal of Applied Ecology*, **60**, 2144–2153, https://doi.org/10.1111/1365-2664.14499

Zhang, Y., Li, J., Zhang, D., Wang, Z., & Yi, X. (2019). Effects of grazed stubble height and timing of grazing on resprouting of clipped oak seedlings. *Agroforestry Systems*, **93**, 295–304. https://doi.org/10.1007/s10457-018-0206-x

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.

grazing	grazing history	grazing pressure	no. of paddock	survivals			deaths			total
				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; $\beta<>0$ = 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	$\beta<>0$	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	$\beta<>0$	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.