***Title*: Cattle grazing alters how cork oak crop failure leads to faster and farther rodent-mediated acorn dispersal**

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Abstract

1. Masting, the reproductive strategy of many perennial plants with variable and synchronized inter-annual seed production, often occurs in grazed systems and is occasionally interspersed with years of extreme crop failure in which few plants remain fecund. Crop failures are becoming more stochastic or common with climate change. Yet, our understanding of the potential costs of the combined effects of crop failure and grazing on seed dispersal and seed-to-seedling transition remains limited.
2. We conducted this study in central Portugal within a silvopastoral system with masting cycles and experiencing a Mediterranean-wide decline partially associated with overgrazing. We tracked the rodent-mediated dispersal of cork-oak (*Quercus suber*) acorns until seedling emergence in years with contrasting masting seasons in cattle grazed and non-grazed areas.
3. Extreme crop failure resulted in six times longer and faster seed dispersals and 83% more dispersal events, although, consistent with the predator satiation hypothesis, the percentage of predated acorns also increased by 84% as compared to the crop success year.
4. The higher acorn predation in the failure year was offset by a 2.4 times higher percentage of dispersed acorns recruited into seedlings among the unpredated ones, with both years ending up recruiting a similar number of seedlings from the tracked acorns.
5. Seedlings from the tracked acorns emerged 3.4 times farther in the failure year than in the crop success year.
6. Cattle grazing was the main negative factor affecting seed dispersal distance by reducing it by 51% during the extreme crop failure year, whereas it had no noticeable effect during the crop success year.

7. *Synthesis*. Our study provides empirical evidence that cattle grazing can modulate how an extreme crop failure year can surprisingly be an opportunity for trees remaining fecund to have seedlings established farther apart than in a crop success year. If we are to better manage and preserve the high conservation and socio-economic value of Mediterranean cork oak woodlands in the face of climate change, we must recognize and pay particular attention to controlling seed dispersal drivers such as cattle grazing around fecund trees in years of crop failure.

Key words: plant–animal interactions; seed dispersal; Mediterranean ecosystem; grazing; oak; mast seeding.

1. INTRODUCTION

The reproductive strategy of many perennial plants consists of highly variable and synchronized inter-annual seed production (i.e., masting; Kelly, 1994). The benefits of masting have been explained by well-supported hypotheses relating to economies of scale of seed production (Pearse et al., 2020). Predator satiation is one of the most prominent explanations, stating that mast years enhance pre-dispersal seed survival by satiating seed predators (Silvertown, 1980; Kelly and Sork, 2002; Huang et al., 2021; Zwolak et al., 2022). However, there is little empirical data on intermast years of widespread crop failure despite its potential consequences for plant regeneration (Koenig, 2021). Because climate change is increasing or making extreme crop failure events more stochastic (Hanley et al., 2019; Bogdziewicz et al.; 2020a, 2021; Bogdziewicz, 2022), we must know more about seed predation, dispersal, and seedling establishment in these years compared to years of successful masting. This knowledge is becoming utterly essential in Mediterranean climates where masting dynamics is changing under progressive warming and acorn crop failures in oak woodlands are increasing (Fernandez-Martinez et al., 2012; Pérez-Ramos et al., 2015; Chemnitz, 2019).

Seed masting and dispersal often occur in grazed forest systems (Koenig et al., 2013). Grazing by wild and domestic ungulates is likely to affect seed availability, seed predation and dispersal, and diminish tree-seedling establishment (Levey et al., 2002; Pulido & Díaz, 2005; Leal et al., 2022). Yet, the consequences of ungulate grazing for animal-mediated seed dispersal in contrasting crop successful and failure years have been overlooked. Research shows scatter-hoarding rodents respond to the presence of large ungulates (Smit et al., 2001; Torre et al., 2007; Bush et al., 2012; Navarro-Castilla et al., 2017), but how grazing impacts on distance and time to rodent-mediated seed

dispersal remains largely unknown (Muñoz & Bonal, 2007). Both short and long seed dispersal distance events are key to the recruitment process and thus for the population persistence and expansion (e.g., Janzen, 1970; Connell, 1971; Clark et al., 1999; Vaz et al., 2019). Also, the time mediated between seed shedding and dispersal is critical to its survival, determining pre-dispersal exposure to predators and pathogens, desiccation, and, ultimately, non-viability (Hadj-Chikh et al., 1996; Walter et al., 2013). Particularly, there is a lack of empirical data comparing seed dispersal in grazed and ungrazed areas having different times since grazing (Listopad et al., 2018).

Some studies have emphasized the effects of several primary explanatory variables on rodent-mediated seed dispersal in oak-dominated systems with masting reproduction. Very few, however, have compared their effects between years of acorn crop success and failure (Puerta-Piñero et al., 2010). The microhabitat where the acorn is prior to dispersal, in open areas or underneath shrubs, can be of primary importance for the dispersal carried out (Pérez-Ramos & Marañón, 2008; Garcia-Hernández et al., 2016). The microhabitat of arrival (open or shrub) is also a potential explanatory variable of the acorn dispersal distance and fate (Perea et al.; 2011a; González-Rodríguez & Villar, 2012). Acorns are major food resources for rodents and both distance and time to dispersal are likely to be influenced by the acorn size (Gómez et al., 2008; Morán-López et al., 2018). As rodent abundance influences the number of interactions with acorns, rodent density is also a variable to consider in acorn predation and dispersal (e.g., Sunyer et al., 2013, 2014; Navarro-Castilla et al., 2017).

Cork oak (*Quercus suber*) Mediterranean woodlands are multiple use silvopastoral systems with masting cycles, where animal-mediated acorn dispersal is critical to the ecosystem sustainability (Pons & Pausas, 2006; Aronson et al., 2009; Campos et al., 2013). Cork oak woodlands are classified as “high nature value farming systems” and

have high conservation and socio-economic value (Paracchini et al., 2008; Bugalho et al., 2011). In the last decades, a severe lack of regeneration and increased mortality have been reported for cork oak, which may be endangering cork oak woodlands (Brasier, 1992; Plieninger et al., 2010; Fedriani et al., 2017; Vaz et al., 2019). Oak recruitment depends on multiple factors including acorn crop size, predation, dispersal, and seedling establishment (Pulido and Díaz, 2005). The understory is usually grazed by ungulates and dominated by grasslands and shrubs. In the Euro-Mediterranean, acorn dispersal is mainly carried out by rodents and by the European jay (*Garrulus glandarius*), although the latter is less common or absent in lower density cork oak woodlands (Herrera 1995; Pons & Pausas, 2008).

In this study, to integrate masting and grazing effects, we tracked the dispersal of cork-oak acorns until seedling emergence in years with contrasting masting seasons in grazed and non-grazed areas of central Portugal. Our empirical approach aims to elucidate rodent-mediated seed dispersal in years of extreme widespread acorn crop failure. Because ungulate grazing is a major factor influencing the seed-to-seedling transition phase of plant regeneration (Leal et al., 2022) and has a marked influence on seed-dispersing rodents (Smit et al., 2001), we assess also the effects of long-term livestock grazing exclosures (> 10 years) on distance and time to acorn dispersal. We addressed the following questions and hypotheses:

1) How does rodent-mediated acorn dispersal (distance and time to event) differ between failure and successful crop years? Because in failure crop years acorns are scarce food resources, we hypothesized that the time to dispersal would be shorter and the dispersal distance longer, as rodents would quickly move acorns farther away from conspecifics.

2) Does cattle grazing influence rodent-mediated acorn dispersal? As ungulate grazing can reduce habitat quality (Muñoz et al., 2009) and increase rodent stress, likely leading to shorter movements, we hypothesized that grazing would negatively affect acorn dispersal distance (Gallego et al., 2017; but see Muñoz & Bonal, 2007).

3) Whether and how does rodent density influence acorn dispersal? We hypothesized that higher rodent densities would increase the likelihood of acorn encounters, which would be reflected in shorter distances (Sunyer et al., 2013) and times to dispersal (Smit et al., 2001).

4) What are the effects of acorn size (weight) and type of microhabitat (open areas or underneath shrubs) on rodent-mediated dispersal? Overall, heavier acorns would disperse first and farther (Gómez et al., 2008; Perea et al., 2011b). As rodents prefer shrubs to open areas in Mediterranean oak woodlands (Gray et al., 1998; Rosalino et al., 2011), we hypothesized that acorns underneath shrubs would disperse faster and closer than those in open areas.

2. MATERIALS AND METHODS

2.1. Field methods

2.1.1. Study area

The study area is in central Portugal (38º49'49.526 "N 8º49'15.899 "W), in 11000 ha dominated by cork-oak woodlands known in Portugal as *montados* (*dehesas* in Spain) within the state-owned farm Companhia das Lezírias (CL), a Long-Term Socio-Ecological Research Site (LTSER; Listopad et al. 2018). LTSER sites are designated for long-term socio-ecological research, namely for monitoring and storing relevant data in ecology. Since the XIX century, CL has been managing cork-oak *montados* for cork harvesting, cattle raising, hunting, and, lately, for biodiversity conservation. In different

years, some CL *montado* areas have been fenced recently to exclude grazing by cattle and to foster oak natural regeneration. Grazing exclusion provides an opportunity to explore the interactions between grazing and rodent-mediated acorn dispersal overtime.

The climate in the study area is Mediterranean, with hot, dry summers and cool, wet winters. Mean annual precipitation is 608 mm and mean annual temperature is 16 °C. The slopes are mild, and the altitude range from 1 to 53 m. Soils are well-drained deep Haplic Arenosols (WRB, 2006) with low soil water retention capacity. Cork-oak trees in CL have 24–49 % canopy cover (Listopad et al., 2018). Cork-oak acorns usually fall from late September to early December. Understory vegetation is sparse shrubland dominated by *Ulex australis*, *Cistus salviifolius*, *Myrtus communis*, *C. crispus*, *Genista triacanthus*, and *C. ladanifer*. The grassland understory in open areas include annual species, dominated by the forbs *Tolpis barbata* and *Plantago bellardii*, the graminoids *Agrostis pourretii* and *Avena barbata*, and the legumes *Ornithopus compressus* and *Trifolium arvense*. The wood mouse (*Apodemus sylvaticus*) and the Algerian mouse (*Mus spretus*) are the main acorn dispersal rodents in the sites (see Gonçalves et al., 2013). The main acorn predators in CL are year-round grazing wild boars (*Sus scrofa*), Iberian pigs (*Sus scrofa domesticus*) grazing freely outside the grazing exclosures between October and December, and sporadically fallow deer (*Dama dama*).

2.1.2. Experimental design

To evaluate the effects of grazing on acorn dispersal distance and time to dispersal (hereafter acorn-dispersal), we selected nine pairs of sites, each pair including one grazing exclosure site and one cattle-grazed site. To explore the effect of exclosure duration on acorn-dispersals, the nine ungrazed sites included three sites of each not grazed since 1997, 2004, and 2008, hence 21-, 14-, and 10-year grazing exclosure by

the beginning of the experiment. Across sites, cork-oak trees have a mean basal area of 13.0 m^2/ha (± 0.6 SE) and a density of 53.6 trees/ha (± 1.2 SE) (Mexia et al., 2022). The distance from any site pair to the nearest one averaged 1191 m (± 488 SE; range = 255–4720 m). Within site pairs, the mean distance between the grazed and the ungrazed site was 407 m (± 70 SE; range = 218–912 m). Within each site, we haphazardly selected two focal cork-oak trees (≥25 cm DBH) 102 m apart (± 3 SE; range = 93–137 m). Because long-distance acorn dispersals (e.g., > 20 m) by our target rodent species are likely to be rare (Pons & Pausas, 2007a; Morán-López et al., 2018), we anticipated ~100 m to ensure independence in the acorn-dispersals between the site's cork-oak trees. To evaluate the effect of microhabitat on acorn-dispersal, the 36 oaks had at least one shrub of the locally dominant species and an open area with only litter and grasses under the tree canopy. The dominant shrubs used as microhabitat were *Ulex* spp. (mainly *U. australis*) on all but three cork-oaks where the species were *M. communis*, *G. triacanthus*, and *C. ladanifer*. All selected oaks were >50 m from a barbed-wire fence.

To assess the effects of microhabitat (open / shrub) on acorn-dispersal, we placed two pairs of acorn supply stations under the cork-oak canopy, one pair under shrub canopy and the other pair in the open area 1 m away from the shrub. Shrub cover has not changed over the duration of the study around our focal cork-oaks. The paired stations were of two types and were located ~50 cm apart from each other. To isolate the effect of rodents, one station was protected from birds and large herbivores with a 32 × 25 × 12 cm wire cage (1.4 cm mesh size) and the other was left unprotected (i.e., incage / outcage). To allow rodents to the interior, the wire cage had two 5 × 5 cm entrances. We used an 8-mm diameter and 40–70 cm long iron rod to attach the cage to the ground, ensuring that none were displaced during the study.

In 2018, we collected ~2000 ripe acorns from CL cork-oaks on November 12–13. In 2019, given the extreme failure of cork-oak acorn production in the study region, we collected ~2000 ripe acorns from cork-oaks within a 100 km radius of CL on November 5–9. As the natural shedding of acorns coincides with their full maturity, we sought to make the collection match this moment (Merouani et al., 2003). So, we collected acorns on the tree that fell very easily from the cupules or recently fallen on the ground with a homogeneous brown color and no signs of desiccation. To discard weevil-infested acorns, we mixed and then floated them all in water. For the labeling, we drilled a 1-mm hole in the acorn without damaging the embryo, through which we inserted a 3-cm long wire (0.6 mm diameter). For easy relocation, we attached a 14.5 × 1.6 cm yellow numbered plastic label to the wire. This tagging method does not alter acorn dispersal patterns and yields a high recovery rate (Xiao et al., 2006). The weight of the acorn was then recorded to the nearest 0.01 g, with the labeling corresponding to 6–15% of the total weight.

We placed five labeled acorns on the ground per supply station, totaling 1440 acorns (5 acorns × 2 station types × 2 microhabitats × 36 oaks × 2 years). The tracking of each acorn began the day after the supply. We tracked cork-oak acorns during the 2018–19 and 2019–20 seasons, from November 17 to March 18 in the first year and November 12 to January 31 in the second year. In the first year, we monitored the acorns daily until day 9, then every 4 days until day 25, weekly until day 89, and biweekly until day 119. In the second year, we tracked the acorns on day 1, then every 2 days until day 9, every 4 days until day 25, weekly until day 48, and biweekly until day 78.

2.1.3. Data collection

On every visit, we recorded each acorn dispersal location and any event that occurred on it. We searched for acorns within a minimum radius of 50 m around the supply station, adding another 30 m centered on a found acorn. Our detection effort was similar throughout the open areas although we increased search effort for acorns located under shrubs, aiming to compensate for the potentially lower tag detectability in this microhabitat. We measured the distance from the acorn to the supply station (dispersal distance) with a laser meter and a target or with a meter tape, both 1-mm precision. For easy relocation, we marked every acorn location with a labeled stick (30–50 × 0.3 cm) (Xiao et al., 2005). To examine whether the acorn-dispersal would vary with the microhabitat of arrival, we documented if the microsite of acorn deposition on that visit was an open area or under a shrub.

We considered that there was an event if the acorn was moved, gnawed or predated (eaten), cached (e.g., hidden in a log or buried in the ground), or went missing. Intact acorns in the station were considered non-events. Acorns predated while still in the supply stations were omitted from the dispersal distance and time to dispersal analyses. We removed depredated acorns from the study area and assigned them their latest dispersal distance. We deemed an acorn depredated when totally or partially consumed with the embryo damaged. From the first week on, acorns with severely wrinkled skin (dehydrated), very discolored (yellowish), and clearly hollow when carefully pressed were considered non-viable and thus removed.

To evaluate the effect of cork-oak crop size on the acorn-dispersal, we used visual surveys on the 36 cork-oaks prior to significant acorn fall in each late September (Koenig et al., 1994). Visual survey is rapid, effective, and has been validated in predicting acorn production in similar agroforestry systems in the Iberian Peninsula (Carevic et al., 2014). Per cork-oak, we obtained the crop size from the sum of acorn

counts for 8 seconds in each orthogonal direction of the crown, totaling 32 seconds. One observer completed all the counting.

To examine the effect of rodent density on acorn-dispersals, we conducted three live-trapping sessions of four consecutive nights per cork-oak, before (April 2018), between (May 2019), and after the two-year acorn tracking seasons (January 2020). Per session, we set six Sherman traps (8 × 9 × 23 cm) within a 30 m radius of each focal oak, totaling 216 traps (6 traps × 36 trees). We positioned the six traps ≥10 m apart in variable arrangements, each under a shrub to maximize number of captures and thus to attain most accurate estimates of rodent density (Fedriani, 2005). Trap locations were marked on the shrubs with tape and geo-referenced using a GPS unit with 0.3–1 m precision by post-processing. Each trap was set on the first day, baited with a bread toast (4 x 4 cm) with peanut butter, and checked every day at sunrise.

We marked the captured mice individually with a permanent tattoo on their tails (Chen et al., 2016) and released them at their respective capture locations. For marking, we kept the animal restrained without anesthesia within a thick transparent and well aired bag, with only the tail exposed for tattooing. Each tattoo was done using 1-mL syringes and 30-gauge needles replaced between animals and typically took less than 3 minutes. We used green and red human tattooing inks from Killer Ink Limited (Liverpool, UK). The whole procedure was previously authorized (License 332/2018/CAPT) and reviewed by the animal care committee of the Portuguese Institute for Nature and Forest Conservation (ICNF - Instituto de Conservação da Natureza e das Florestas). Mouse capture and handling were in compliance with Directive 2010/63/EU on the protection of animals used for scientific purposes.

2.2. Statistical analyses

2.2.1 Dispersal distance

To assess potential inter-annual differences in the dispersal distance we used the Mann-Whitney test. Specifically, we tested the null hypothesis that the probability of a 2019–20 acorn dispersing farther than a 2018–19 acorn would be 50 %. To evaluate the difference in the distance distributions between years, we computed the kernel density estimates and the bootstrap version of the Kolmogorov-Smirnov test, which corrects for ties and discontinuities in the distributions (Sekhon, 2011). Per acorn, we analyzed the final distance to the supply station.

To evaluate the effects of the explanatory variables on the dispersal distance, we conducted generalized mixed-effects modeling in a Bayesian framework. We created the Bayesian models in Stan computational framework (http://mc-stan.org/) accessed with *brms* package in R (Bürkner, 2017). Because the dispersal distance distribution was strikingly different by year and crop size as an explanatory variable was always zero in 2019–20, we modeled the two years separately. We modeled distances as right-censored in the cases of the acorns that went missing, using the *cens* function in *brms*. Since dispersal could eventually occur after the experiment on acorns remaining at the station for the entire time (cached or as non-events), we also modeled them as having right-censored distances. Because dispersal distance was continuously distributed and greater than zero, we used the log-normal family distribution for the 2018 model and the gamma family for the 2019–20 model, both with identity links.

As dispersal distance data were nested by supply station, which were arranged in pairs (incage, outcage), and these in turn were nested by tree, we considered using the three as random factors following that hierarchical order. However, the expected log-predictive density leave-one-out cross-validation difference (Δ ELPD LOO) suggested

adding station pair to random effects did not improve the expected predictive accuracy of the 2018–19 model (Δ ELPD LOO = 0.0 ± 1.7 SE). Thus, the random part of the 2018–19 model included station, while that of the 2019–20 model included all three factors (tree/station pair/station identifiers). The numeric fixed covariates were acorn weight, rodent density, plus crop size in 2018–19.

In both models, the fixed effects included the categorical variables grazing (levels = grazed, 21-, 14-, 10-year exclosure), station type (incage, outcage), supply microhabitat (open, shrub), and arrival microhabitat (open, shrub). Because preliminary exploratory analysis showed the univariate model with grazing having three levels worsened (Δ ELPD LOO = 2.0 ± 1.6 SE) or equaled (Δ ELPD LOO = 0.8 ± 1.8 SE) the predictive accuracy of the 2018–19 and 2019–20 null models, we opted for grazing with two levels (ungrazed, grazed). The correlation matrices by year for the initial explanatory variables revealed no collinearity problems (≤ 0.63 in all cases).

The minimal adequate (optimal) models were arrived at by first fitting the full models (using all explanatory variables simultaneously) followed by backward elimination of one explanatory variable at a time. We used Watanabe-Akaike Information Criterion (WAIC; Watanabe, 2010) to compare the relative fit of the models to the data, interpreting WAIC differences greater than twice its corresponding standard error as suggesting that the model with the lower WAIC fitted the data substantially better (Vaz et al., 2021). In 2018–19, rodent density and grazing were dropped in that order using the WAIC criterion to reach the optimal model with station type, arrival microhabitat, crop size, and acorn weight. In 2019–20, the dropping order was rodent density and station type, to reach the model with grazing, supply microhabitat, arrival microhabitat, and acorn weight.

To improve convergence while controlling against overfitting, we assigned weakly informative priors to all the effect size beta parameters of the two models (see Gelman, 2022). For the 2018–19 model, we used the *normal (0,3)* distribution for the beta in all levels of categorical variables and the *normal (0,2)* for the beta in the numeric variables except acorn weight wherein we used the *normal (0,1)*. For 2019–20, we used the *normal (0,3)* distribution for the beta parameters in all the variables except for rodent density and acorn weight, wherein we used *normal (0,2)* and *normal (0,1)*, respectively. For each model, we ran four parallel MCMC chains until convergence was reached (all Rhat ≤ 1.1). Each chain had 4000 iterations (warmup = 1000, thin = 1), totaling 12000 post-warmup samples. We assessed model adequacy using posterior predictive checks. Prior to all the analyses, we centered and standardized the numeric covariates. We performed all analyses in R v. 4.1.1 (R Core Team, 2021).

Through Bayesian statistical inference, we estimated the β parameters of the models, their credible intervals, and tested statistical hypotheses (e.g., McElreath, 2018). As the Bayesian inference returns a distribution of possible effect values (the posterior), the credible interval is the range containing a particular percentage of probable values (e.g., 95%). After we have computed the posterior distribution for β, we have interrogated it directly. For instance, if 99% of the posterior distribution is above 0, we are 99% confident that $\beta > 0$, $P(\beta > 0) = 0.99$, and 1% confident that $\beta < 0$ (Azedo et al., 2022).

2.2.2 Time to dispersal

To investigate the association between time to acorn-dispersal and the set of explanatory variables, we used Cox proportional hazards frailty modeling (Therneau and Grambsch, 2000). The response variable was the number of follow-up days until the dispersal event and was modeled as right-censored due to the uncertainty that the

dispersal could eventually occur after the experiment in some acorns. Because the distributions of the response variable were remarkably different by year and the 2018–19 model had crop size as an additional predictor, we ran a model by year. We used the same full set of fixed covariates by year as in the two full Bayesian models for dispersal distance. However, the correlation matrices by year revealed supply microhabitat was strongly correlated with arrival microhabitat in 2018 (r_{φ} = 0.82) and was excluded from this year's Cox models to prevent collinearity. The effect of supply station was accounted for by including it into both models as a random proportionality factor ("frailty"). Adding station pair to the random effects would have significantly worsened both the 2018–19 (χ^2 = 417.05, P < 0.0001) and 2019–20 (χ^2 = 261.18, P < 0.0001) Cox model fits (*anova* command in the *coxme* package in R; Therneau, 2020).

To fit the two Cox models, we used the *survival* package in R (Therneau, 2021). The significance (chi-square test; P < 0.05) of each predictor was evaluated by backward-stepwise elimination from the full model (Therneau & Grambsch, 2000). In 2018–19, crop size, acorn weight, grazing, and station type were sequentially dropped to reach the optimal model with arrival microhabitat and rodent density. In 2019–20, the dropping sequence was supply microhabitat, acorn weight, station type, and rodent density, reaching the optimal model with grazing and arrival microhabitat. To infer the expected durations for acorn first dispersals with estimates of uncertainty by covariate from the two Cox models, we used the *coxed* package in R, via the nonparametric step-function approach (Kropko & Harden, 2020).

2.2.3 Rodent density

To calculate the rodent density (ha^{-1}) per year associated to each of the 36 cork-oaks, we used the multi-session dataset from the livetrappings. We used spatially explicit

capture-recapture models (Efford, 2004; Borchers & Efford, 2008) fitted via the maximum likelihood method using the *secr* package in R (Efford, 2022a). We used the half-normal detection function for the detection probability. Half-normal has *g0* (encounter rate) and σ (scale for *g0* decreasing with distance to the home-range center) parameters, defining the detection as a function of location. To model *g0*, we ran six models considering the individual effects (learned or transient responses) of animals, traps, and interactions of both (for details, see Efford, 2022b). We modeled σ as a constant in all cases. To select among the six models plus the null model (having constant *g0* and σ), we used the Akaike Information Criterion (*AIC* command in *secr*). Following the AIC, we estimated rodent density considering trap-specific responses on the encounter rate ($g0 \sim k$; see Efford, 2022b).

3. RESULTS

Sixty-seven percent of the 1440 acorns supplied in the two years were dispersed. The mean dispersal distance from the supply station was 5.91 m (median = 2.01 m, range = 0.01–45.78 m). Between the two years with contrasting masting seasons, the dispersal distance and its distribution (Fig. 1A) differed significantly ($U = 38932$, $p < 0.0001$; $D = 0.57$, $p < 0.0001$). In the failure acorn production year (2019–20), the mean dispersal distance (mean = 8.34, median = 4.63, range = 0.10–45.78 m) increased 6 times compared to the succeeded acorn production year (2018–19) (1.46, 0.45, 0.02–22.90 m). In 2018–19, 52.4% of the 720 acorns did not disperse while in the crop failure year only 12.6% of the 720 acorns were not moved. Further, 75% of the acorns dispersed ≤1.05 m only in 2018–19, while that 75th percentile was 12 times higher in 2019–20 (12.53 m). Ten percent of the 2019–20 dispersals were longer than the maximum dispersal in 2018–19.

The first acorn-dispersal occurred on average at day 10 (median 3 days). Between years, the mean duration until dispersal (Fig. 1B) was ~6 times shorter in the acorn crop failure year (mean = 4, median = 3 days) than in the succeeded crop year (mean = 22, median = 9 days). Also, all acorns dispersed by day 17 in 2019–20, but not until day 104 in 2018–19.

Predation was the most frequent final acorn fate in both years, especially among dispersed acorns (Table 1). Noticeably, 80.8% of the supplied acorns were predated in the second year (cork oak crop failure year). Seventeen and 13% of acorns went missing in 2018–19 and 2019–20, respectively. Missing acorns were more frequent for undispersed than for dispersed ones. In both years, barely ~1% of the acorns emerged seedlings. In 2018–19, seven seedlings emerged between February 12 and March 16 (i.e., mean = 49 days after supply; range = 29–104). In 2019–20, eight seedlings emerged between January 14 and 31 (72; 63–78). The percentage of dispersed acorns recruited into seedlings was 7% (7÷(343-244)×100), Table 1) and 17% (8÷(629-582)×100) in the success and failure years, respectively. The mean station to seedling distance was 3.17 (range = 0.27–18.75 m) and 10.76 m (0.40–32.00 m) in the success and failure years.

The mean density of dispersing rodents estimated via spatially explicit capture-recapture models on the 36 focal trees was 18 (95% CI =15–22) and 9 (8–11) individuals ha^{-1} in the succeeded and failure crop years, respectively.

3.1 Dispersal distance

When we accounted for distance censoring and the effect of random factors, the predictors of dispersal distance differed in the two optimal Bayesian mixed models (Table 2, Fig. 2). Only arrival microhabitat and acorn weight had evident effects on

dispersal distance in both years. Mean dispersal distances were 65% (2018–19) and 72% (2019–20) longer in acorns dispersed into open areas than into shrubs. As expected, heavier acorns dispersed farther. For example, a weight increase from 4 to 8 g corresponded to 38% and 46% increases in dispersal distance in 2018–19 and 2019–20, respectively.

In 2018–19, acorns offered to rodents only (incage supply stations) dispersed 1.7 times farther (posterior distribution mean = 1.89; 95% CI = 1.21–3.02 m) than outcage acorns (1.11; 0.80–1.59). This year, it was also evident that dispersals went farther in trees with smaller crop sizes. For example, tripling the acorn count from 4 to 12 led to 35% shorter dispersal distances. This result was in line with the farther dispersals in the cork-oak crop failure year than in the succeeded crop year.

The expected impact of grazing was only evident in 2019–20, the failure year, when it was the variable with the largest negative effect on dispersal distance (Fig. A.1, Appendix 1). The mean of the posterior distribution in 2019–20 was 6.88 m in the grazed sites (95% credible interval = 4.80–9.88), whereas it was 14.12 m in the grazing exclosures (9.80–20.40). Thus, cattle grazing reduced dispersal distance by 51%. This year, acorns supplied in open areas also dispersed 1.3 times farther (14.12; 9.80–20.40 m) than those provided under shrubs (10.49; 7.18–15.11 m).

3.2 Time to dispersal

Time to first dispersal had also arrival microhabitat as an important predictor in both years, although with surprisingly opposite effects (Table 3, Fig. 3). Relative to open areas, shrubs were associated with 71% shorter and 21% longer times in 2018–19 and 2019–20, respectively. The expected negative effect of rodent density on time to first dispersal was evident in 2018–19, particularly up to a density of ~10 ha^{-1}. Last, as with

dispersal distance, the effect of grazing on the velocity of first dispersal was only evident in the crop failure year (2019–20). The mean time to first dispersal was 1.3 times faster at grazed sites (mean = ~3; 95% CI = 3–4 days) than ungrazed sites (~5; 4–5 days).

4. DISCUSSION

Our results provide new insights on masting dynamics within climate change context and about increasing intermast events of widespread crop failure. Our data show that a year of extreme crop failure can strikingly affect animal-mediated seed dispersal, both through seed scarcity effects and because primary significant covariates may be different or have very different effects from those occurring during a successful crop year. By combining crop success and grazing effects in a Mediterranean silvopastoral system, we found evidence of cattle grazing effects on the distance and time to cork oak acorn dispersal but only during the extreme crop failure year. This year had six times longer and faster seed dispersals and 83% more dispersal events, although, consistent with the predator satiation hypothesis, the percentage of predated acorns also increased by 84% as compared to the success year. Our results suggest predation/dispersal (distance and velocity) trade-offs, as the net outcome for the early cork oak demography was surprisingly similar in such contrasting masting seasons, with 1% of acorns recruiting into seedlings.

4.1 Crop size and extreme failure

Our results showed that acorns in the less productive cork oak trees during the crop success year were also dispersed farther. This is consistent with the much longer dispersal distances observed during the failure year. Although past studies on seed dispersal have rarely focused on years of extreme crop failure, our inter-annual result is

in line with research obtained for holm oak (*Quercus ilex*) documenting a less clumped pattern of dispersed seeds in a small crop size year (Puerta-Piñero et al. 2010). Our inter-tree seed dispersal comparison is compatible with few studies documenting shorter dispersal differences with increased seed abundance (Jansen et al., 2004; Moore et al., 2007). As the success year had simultaneously twice the rodent density and far fewer dispersal events, our results also countered the so-called predator dispersal hypothesis (Vander Wall & Balda, 1977; Vander Wall, 2010), predicting that larger crops may imply higher per capita seed dispersal rates or longer dispersal distances than in non-masting years (Seget et al., 2022). Our data better support the predator satiation hypothesis as mechanism of mast seeding in cork oak woodlands. This adaptation to predator satiation is common in forest stands dominated by one species (Kelly & Sork, 2002). In mixed species stands with cork oak trees, it may be possible that the availability of other tree species' seeds may contribute to satiate predators in years of cork oak crop failure. Some studies have compared seed predation between monospecific and mixed forest stands in masting years, but not in extreme crop failure years (Smith, 1987; Hart, 1995; Curran & Webb, 2000).

We suggest that the few acorn-producing cork-oak trees in the year of widespread extreme crop failure may have had more effective dispersals among their acorns escaping predation than in the success year. We simulated the presence of such fecund trees by supplying acorns in our focal trees in the failure year, although true highly fecund individuals tend to be large, old trees producing more and larger acorns as compared to our focal trees (see Bogdziewicz et al., 2020b). Noticeably, the higher predation in the failure year was offset by a 2.4 times higher percentage (17 vs. 7%) of dispersed acorns recruited into seedlings among the unpredated ones, with both years ending up recruiting a similar number of seedlings from the supplied acorns.

Importantly, seedling emergences occurred ~3.4 times farther in the failure year than in the success year. As only 1.5% of the dispersed acorns were cached in each year, caching likely had a negligible effect on decreasing the proportion of predated acorns (Vander Wall, 2002; Xiao et al., 2013, Zwolak et al., 2016).

4.2 Grazing and extreme crop failure

Our data showed mixed effects of cattle grazing on acorn dispersal in the year of extreme crop failure. On the one hand, grazing was the main negative factor affecting seed dispersal distance by reducing it by 51%. Grazing, therefore, seems to attenuate the potential of fecund trees to establish seedlings farther away in crop failure years. On the other hand, by reducing the time to dispersal by 30%, grazing had the potential to increase the survival of acorns quickly moved to adequate microsites, since cork oak is a fast-germinating species when conditions are favorable (Amimi et al., 2020). Yet, as shown by a recent meta-analysis of Mediterranean-wide datasets, acorns are much less likely to survive in the presence of ungulates (Leal et al., 2022). It remains possible that an overall low probability of acorn survival in grazed areas, possibly associated with ungulate predation and lower availability of potential recruitment microsites (Clark et al., 1998; Levey et al., 2002; Gómez et al., 2003) in the study area, may obviate the arguable advantage of the higher dispersal speed shown in our data in a crop failure year. The faster speed of acorn dispersal may further be outweighed by negative impacts of grazing at later oak life stages (Pulido & Díaz, 2005), namely seedling trampling and seedling and sapling browsing (Cierjacks & Hensen, 2004; Muñoz et al., 2009; Parsons et al., 2021).

4.3 Further effects

We also show how the effects of other factors known to make animal-mediated seed dispersal a non-random spatiotemporal process (Pérez-Ramos & Marañón, 2008) can vary from a success to a crop failure year. For example, our hypothesis that acorns underneath shrubs would disperse faster was supported by the result of the arrival microhabitat variable in the success year, but not in the failure year when acorns were moved 21% faster into open areas than into shrubs. As acorns are high nutritional value resources (Pons & Pausas, 2007a), which are scarce in failure years, a possible explanation for that result is an attempt by rodents to quickly escape the increased acorn predation pressure by other rodents beneath shrubs (García-Hernández et al., 2016) at the cost of increased risk of their own predation in open grasslands (Sunyer et al., 2016). Similar trade-offs were previously described between higher risks of rodent seed predation beneath vegetation canopies and reduced cache pilferage in open vegetation (Preston & Jacobs, 2005; Muñoz & Bonal, 2011; Steele et al., 2014). On the other hand, given the higher density and foraging activity of small rodents beneath shrubs (Herrera, 1995) and that most of the acorns in our work were predated, it is not surprising that shorter dispersal distances were found in this microhabitat.

Irrespective of the crop success, larger acorns were dispersed farther away as hypothesized. Some related studies have also established a positive relationship between larger seeds, which offer higher nutritional rewards for rodents than smaller seeds (Smith & Reichman, 1984; Jansen et al., 2002; Vander Wall, 2003), and dispersal distance (Gómez et al., 2008; Puerta-Piñero et al., 2010; Perea et al., 2011b), as well as better seedling performance later on (Seiwa, 2000; Vander Wall, 2001; Gómez, 2004; Moles & Westby, 2004; Cicek & Tilki, 2007). The high individual variation in seed size of many plant species (Herrera, 2009; Wang & Ives 2017) having similar dispersal processes can thus lead to a wide range of rodent-mediated dispersal distances.

Interestingly, as the cork oak is the only oak species with annual and biennial acorns of widely varying sizes on the same tree resulting from distinct flowering times (Elena-Roselló et al., 1993; Ramos et al., 2013), our results may imply an even more pronounced adaptation of the species to farther and closer dispersals, both important for the population persistence and expansion. On the other hand, we found no evidence that larger acorns were dispersed more rapidly in the two contrasting crop years, which may indicate that the positive selection, reflected in greater dispersal distances, occurs after the acorns are handled, and less by visual assessment as in the case of the European jay (Pons & Pausas, 2007b).

5. Conclusions

Our study supplies empirical evidence that extreme crop failure years can be opportunities for fecund cork-oak trees to have seedlings established farther apart and in similar abundance as in a successful crop year through greater emergence rates among the fewer acorns escaping predation, associated with more and faster dispersal events. We also revealed that cattle grazing can markedly alter seed dispersal patterns during an extreme crop failure year, strongly decreasing the distance and increasing the speed of cork oak acorn dispersal, whereas it had no noticeable effect during the successful crop year. While acorn crop failures in many oak woodlands are increasing and the severe decline of Mediterranean oak silvopastoral systems partially attributed to overgrazing continues, this previously unnoticed interplay between grazing and crop failure must be highlighted. If we want to preserve the high conservation and socio-economic value of these systems in the face of climate change, we must recognize and pay particular attention to the management of seed dispersal drivers such as grazing in years of crop failure.

Authors' contributions

Pedro G. Vaz: Conceptualization, Investigation, Data curation, Formal analysis, Visualization, Writing – original draft, Writing – review & editing; **Miguel N. Bugalho**: Writing – review & editing. **José M. Fedriani**: Conceptualization, Writing – review & editing.

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Table 1. Final fate of the tracked acorns in years when acorn production was successful (2018–19) and failed (2019–2020).

		Year	
		2018-19	2019-20
Final status		% (count)	% (count)
Dispersed	predated	33.9 (244)	80.8 (582)
	cached	1.5 (11)	1.5 (11)
	moved only	7.9 (57)	0.4 (3)
	missing	3.3 (24)	3.5 (25)
	seedling	1.0 (7)	1.1 (8)
	Total	*47.6 (343)*	*87.4 (629)*
Undispersed	predated	11.5 (83)	2.8 (20)
	cached	0.4 (3)	0.1 (1)
	no event	26.7 (192)	0.0 (0)
	missing	13.8 (99)	9.7 (70)
	seedling	0.0 (0)	0.0 (0)
	Total	*52.4 (377)*	*12.6 (91)*
Total		*720*	*720*

Table 2. Fixed part of the two optimal mixed-effects Bayesian models predicting the effects of cattle grazing and covariates on the dispersal distance of cork-oak acorns in years when acorn production was successful (2018–19) and failed (2019–2020). CI = credible interval for the β parameter (the range containing 95% of probable values); β<>0 = probability of confidence that the effect is positive (if $\beta > 0$) or negative ($\beta < 0$). Potential scale reduction factor on split chains (Rhat) was 1.00 in all parameters.

Model / Variable	β	Error	2.5% CI	97.5% CI	β<>0
Acorn crop success (2018–19)					
Intercept	-0.48	0.17	-0.80	-0.14	1.00
Acorn station type					
incage (reference = outcage)	0.53	0.23	0.09	0.98	0.99
Acorn arrival microhabitat					
shrub (open)	-0.50	0.19	-0.87	-0.14	1.00
Cork-oak crop size	-0.21	0.11	-0.42	-0.01	0.98
Acorn weight	0.17	0.07	0.04	0.31	0.99
Acorn crop failure (2019–20)					
Intercept	2.65	0.19	2.28	3.02	1.00
Grazing					
grazed (ungrazed)	-0.72	0.24	-1.19	-0.25	1.00
Acorn supply microhabitat					
shrub (open)	-0.30	0.14	-0.57	-0.03	0.98
Acorn arrival microhabitat					
shrub (open)	-0.55	0.10	-0.74	-0.35	1.00
Acorn weight	0.15	0.05	0.05	0.26	1.00

Table 3. Optimal survival models by Cox multiple regression for relative "risk" of dispersal on cork-oak acorns in years when production was successful (2018–19) and failed (2019–2020). Supply station was used as a random proportionality factor (frailty). HR = hazard rate.

Model / Variable	β	SE	χ^2	*P*	HR (95% CI)
Acorn crop success (2018–19)					
Acorn arrival microhabitat					
shrub (open)	0.839	0.221	14.40	<0.0001	2.31 (1.50–3.57)
Rodent density	0.443	0.201	4.88	0.027	1.56 (1.05–2.31)
frailty			975.31	<0.0001	
Acorn crop success (2019–20)					
Grazing					
grazed (ungrazed)	0.460	0.163	7.99	0.005	1.58 (1.15–2.18)
Acorn arrival microhabitat					
shrub (open)	-0.317	0.104	9.33	0.002	0.73 (0.59–0.89)
frailty			473.20	<0.0001	

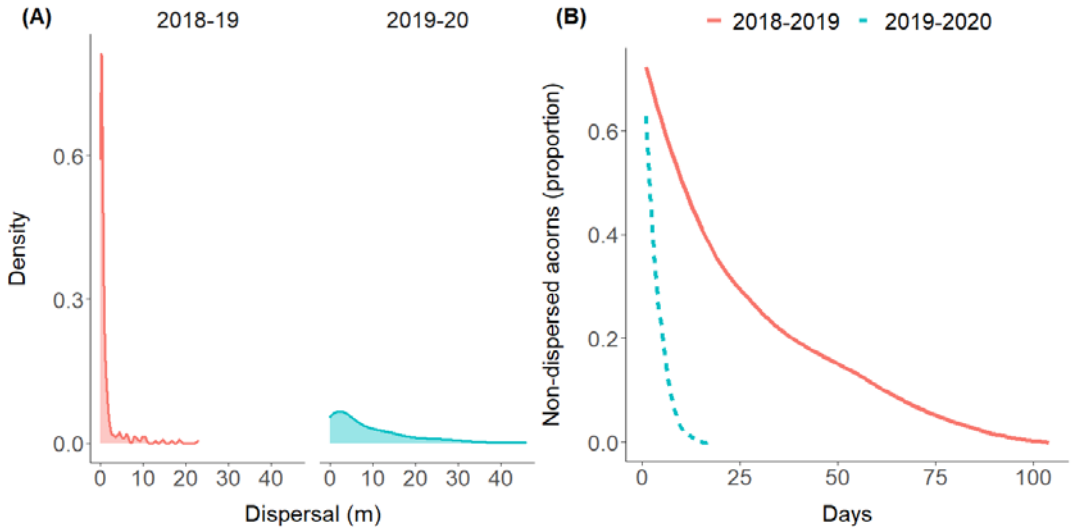

Figure 1. Cork-oak acorn dispersal in years when acorn production was successful (2018–19) and failed (2019–2020). Kernel density of dispersal distance (A); proportion of non-dispersed acorns over time (B).

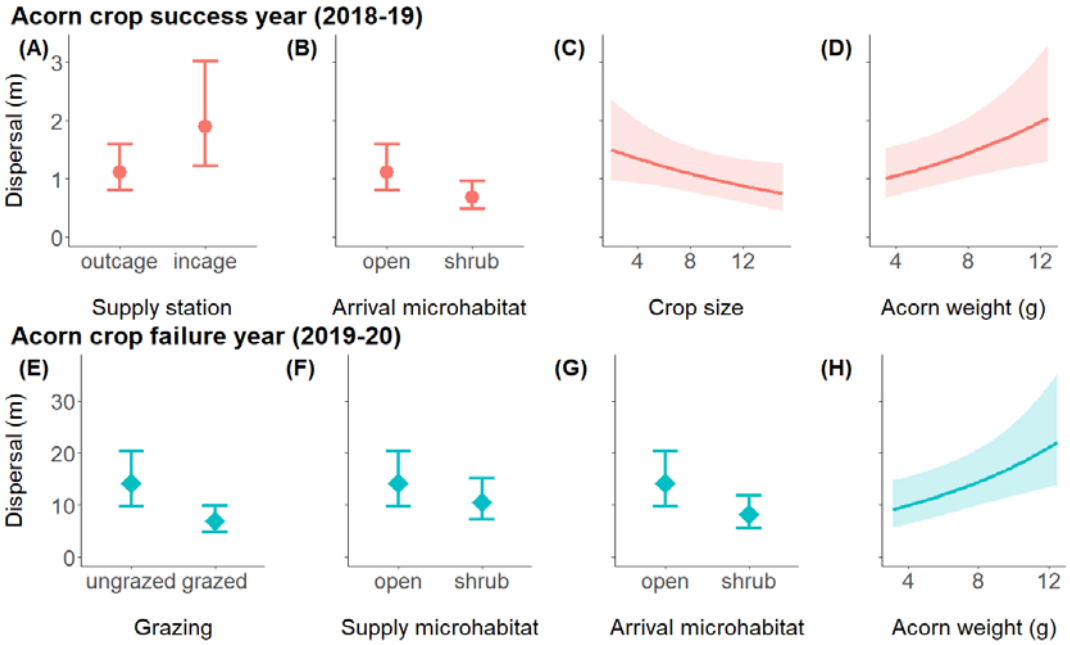

Figure 2. Mean fitted acorn dispersal distances (±95% credible intervals) by grazing and covariates, as predicted by two optimal mixed-effects Bayesian models for when cork-oak acorn production was successful (2018–19; A–D) and failed (2019–2020; E–H). Supply station = type of acorn offering station (inside or outside a wire mesh cage); arrival microhabitat = microhabitat of the latest acorn location (underneath a shrub or in the open area); crop size = acorn count per focal cork-oak (zero on all trees in 2019-20); grazing = cattle grazing; supply microhabitat = microhabitat in which the acorn was offered.

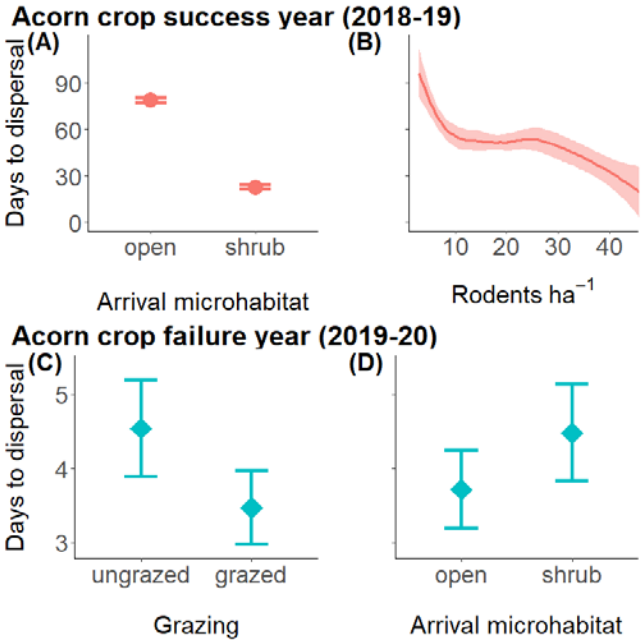

Figure 3. Mean fitted number of days to first acorn-dispersal (±95% confidence intervals calculated via bootstrapping) by explanatory covariates, as predicted by the optimal Cox proportional hazard models with expected durations, when cork-oak acorn production was successful (2018–19; A–B) and failed (2019–2020; C–D). See Fig. 2 for variable descriptions.