Meta-analysis of livestock effects on tree regeneration in oak agroforestry systems

Abdullah Ibne Wadud [a], Miguel N. Bugalho [a], Pedro Gonçalves Vaz [b]

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

[b] cE3c - Centre for Ecology, Evolution and Environmental Changes & CHANGE – Global Change and Sustainability Institute; Faculdade de Ciências, Universidade de Lisboa, Campo Grande, C2, Piso 5, Campo Grande, 1749-016 Lisboa, Portugal

Correspondence: Pedro G. Vaz, tel. (+351) 217500000; e-mail: pjvaz@fc.ul.pt

Highlights

- Livestock reduces oak tree regeneration at acorn, seedling, and sapling stages.
- Small livestock effect more negative, especially acorn survival and young oak density.
- Mixed-size livestock agroforestry systems reduce harm more than small single-size ones.
- We challenge perceptions that replacing cattle with sheep is necessarily less harmful.
- We advocate for diverse livestock sizes in *Quercus*-dominated agroforestry systems.

ABSTRACT

Livestock grazing occupies over a quarter of terrestrial land and is prevalent to agroforestry ecosystems, potentially affecting the survival, growth, and density of trees' early developmental stages, such as seeds, seedlings, and saplings. To address the effects of livestock on tree recruitment in the face of ongoing debates about their impacts, we conducted a 33-year meta-analysis in *Quercus*-dominated agroforestry systems. Our analysis revealed a consistently negative effect of livestock on oak acorns, seedlings, and saplings. Significantly, livestock body size influenced oak regeneration, with small-sized livestock, notably sheep and goats, having a more pronounced negative impact compared to mixed-size systems, mainly involving cattle and sheep. The effects of small-sized livestock were markedly detrimental on acorn survival and seedling/sapling density, although no studies eligible for meta-analysis examined large livestock impacts on acorns. Overall, mixed-size livestock systems, often involving cattle and sheep, lessen the negative effects. Our findings indicate that the body size and foraging behaviors of livestock should be considered for the ecological sustainability of the tree component in agroforestry systems. While protective measures have long been integral to well-managed agroforestry systems, our results underscore the importance of integrating diverse livestock sizes and applying specific protective strategies, particularly for acorns and saplings, to further refine these practices. Future research should expand to underrepresented regions and livestock types to refine global agroforestry management practices.

Keywords: herbivory; wood-pasture; oak woodland; tree mortality; montado; dehesa.

1. Introduction

Livestock grazing occurs on over a quarter of terrestrial land (Taylor and Rising, 2021; FAO, 2023) and is common in agroforestry ecosystems, which merge forestry with agriculture and frequently also with livestock production (Allen et al., 2011). In these ecosystems, livestock of different body sizes and foraging behaviors affect key tree reproductive stages such as seed, seedling, and sapling, altering survival, growth, and density of new tree recruits (Pulido and Díaz, 2005). Thus, managing livestock in agroforestry systems requires balancing production with potential negative effects of livestock on tree life stages (Brown et al., 2018). Analyzing the effects of livestock on tree survival across similar agroforestry systems worldwide may provide better informed sustainable management strategies.

Quercus-dominated agroforestry and silvopastoral systems occur in various parts of Europe, including the Iberian Peninsula (e.g., dehesas and montados), east-central and north-central Europe, as well as in North Africa, North America (e.g., California and Texas), and in Asia (Plieninger et al., 2015; Tantray et al., 2017). These systems span semi-natural and managed landscapes across temperate regions and are particularly valued for their socio-economic and cultural significance as well as associated biodiversity (Pantera et al., 2018; Stavi et al., 2022). They provide a plethora of ecosystem goods including fuelwood, game, crops, and cork (Bugalho et al., 2009), alongside services like biodiversity conservation (Plieninger et al., 2011). Regrettably, they face threats from climate change (Príncipe et al., 2019; Díaz et al., 2021), pathogens (Branco and Ramos, 2009; Brasier, 1992, 1996), phytophagous insects (Branco et al., 2002), wildfires (Moreira et al., 2011; Vaz et al., 2013), and overgrazing (Vaz et al., 2019). These threats contribute to low oak recruitment widely documented

across Europe (Pulido et al., 2001), North America (Rogers et al., 1993), North Africa (Campos et al., 2007), and the Middle East (Dufour-Dror, 2007). Particularly, the impacts of livestock grazing on various early oak life stages remain unsubstantiated globally. Regarding tree regeneration, the process of recruiting individuals to sustain the adult population and counteract mortality losses (Harper, 1977), the impact of livestock on early life stages varies from expected negative (López-Sánchez et al., 2014) to positive effects (Leiva et al., 2022) or even mixed outcomes (Laskurain et al., 2013), with livestock body size and foraging behaviors being important factors (e.g., Ball and Tzanopoulos, 2020). Moreover, while the detrimental effects of overgrazing are well documented, management neglect and grazing abandonment also pose significant threats to the sustainability of oak silvopastoral systems (Bugalho et al., 2011; Plieninger et al., 2015). Overall, the effects of livestock on oak regeneration, including both their signal and magnitude, continue to stir ongoing debate.

Variability in livestock effects on acorn, seedling, and sapling stages, along with differing metrics such as survival, growth, and density, drive the ongoing debate. Acorn survival (viable acorns to become seedlings) is limited by livestock consumption and soil compaction. Yet, livestock activity can bury and aid acorn germination (Leiva and Sobrino-Mengual, 2022). Livestock hinder animal-mediated acorn dispersal (Vaz et al., 2024) but also consume those infested by pests (Canelo et al., 2021). On seedlings, the impact is also complex and fuels the debate. Trampling leads to soil compaction, bare soil, altered litter quality, enhanced soil erosion, reduced nitrogen-fixing species, and hindered seedling establishment (Vázquez, 2002; Etchebarne and Brazeiro, 2016; Cierjacks et al., 2004; Fortuny et al., 2020), reducing seedling density and opposing regeneration niches (Szewczyk and Szwagrzyk, 2010). Conversely, livestock reduce competition from annual grasses and may decrease insect herbivory (Tyler et al., 2008;

Muñoz et al., 2009; Gallego et al., 2017), ultimately benefiting oak seedling survival (Zhang et al. 2019; Vaz et al. 2019). For saplings, frequent grazing and rubbing against them often delay growth and increase mortality (Roula et al., 2019), but moderate grazing deters shrub encroachment, mitigates wildfires (Rouet-Leduc et al., 2021), reduces competition with herbs and shrubs, and may facilitate growth in opening areas (Uytvanck et al., 2010; Reiner and Craig, 2011; Mazzini et al., 2018; Vaz et al., 2019). Notably, goats, often pointed out for the damage they cause to woody vegetation, can nevertheless be used to control invasive species and reduce fire hazards (Ruiz-Mirazo et al., 2011, Mena et al., 2016). Indeed, the maintenance of open habitats by livestock can play a critical positive role in oak recruitment (Bobiec et al., 2018; Wolański et al. 2021).

Beyond an overall effect of domestic livestock, the nuances of body size and foraging behaviors in agroforestry regeneration warrant further examination. In domesticated ruminants, a strong relationship between body size and foraging behavior is to be expected, despite exceptions such as cattle and sheep, which differ in size but are primarily grazers, preferentially feeding on grasses. However, importantly, within the same feeding strategy, differences in body size may lead to varied utilization of plant resources; for instance, sheep can graze closer to the ground than cattle, affecting the ecology of the system differently. On the other hand, smaller browsers like goats preferentially consume woody plants, such as oak seedlings and saplings (Laskurain et al., 2013; Abraham et al., 2018). Moreover, different livestock types can distinctly affect various life stages. Namely, small ruminants, particularly sheep and goats, may have levels of acorn consumption similar to those of wild ungulates (Leal et al., 2022). Particularly, goats are known for consuming acorns (Papachristou et al., 2005; Froutan et al., 2015) and are expected to be more harmful than grazing cattle and sheep,

although these also consume acorns (Papachristou and Platis, 2011; Varga et al., 2020). Historically, goats have often been subject to regulations or even full exclusion because of their browsing behavior and its negative effects on trees and other woody vegetation (Humphrey et al., 1998; Vera, 2000). Considering the effects of livestock size on tree regeneration, some authors recommend smaller livestock like sheep over larger ones like cattle (e.g., López-Sánchez et al., 2016) within the same feeding strategy, as both are grazers. This, however, may not consider other effects such as acorn consumption. A comprehensive analysis of effect magnitudes across varied studies and conditions is essential to clarify whether livestock body size is a significant predictor of their impact on oak regeneration in agroforestry systems.

To address the variability in grazing effects, we conducted a meta-analysis of studies spanning over the last 33 years. This research synthesis compared grazed versus ungrazed areas in *Quercus*-dominated agroforestry systems to discern the influence of livestock on each of the early life stages of oak trees. We tested the following hypotheses. 1) Livestock have an overall negative combined effect on survival of acorns and survival, growth, and density of seedlings and saplings. 2) Livestock effects vary in sign and magnitude among acorn, seedling, and sapling stages. 3) The effect of livestock on early oak stages significantly vary with livestock size, with goats expected to cause more negative outcomes than mixed-size livestock systems. 4) The impact of grazing on oak life stages would differ according to the metric used, with expected less negative effects on survival and greater variability in growth and density metrics due to young oaks' resilience, including their ability to resprout. With this meta-analysis, we not only elucidate the varied impacts of livestock on oak regeneration but also highlight areas for future research and offer insights for the effective conservation and management of *Quercus*-dominated agroforestry systems.

2. Materials and Methods

2.1. Literature review and inclusion criteria

We conducted a literature search using the Clarivate Analytics Web of Science™ database, focusing on articles and review articles published in English between 1990 and July 2023. Our search string combined the keywords "(*Quercus* OR oak*) AND (regenerat* OR recruit* OR seedling* OR sapling* OR establish* OR acorn OR seed*) AND (graz* OR herd* OR pastur* OR brows* OR herbiv* OR predat*)". To narrow down the search to relevant articles, we limited it to the research areas of Ecology, Forestry, Plant Sciences, Biodiversity Conservation, Environmental Sciences, Evolutionary Biology, Biology, and Agriculture Multidisciplinary. The search yielded 2,284 publications, which were subsequently refined following the steps outlined in the PRISMA protocol (Preferred Reporting Items for Systematic Reviews and Meta-analyses; Fig. 1). The refinement ensured the selection of studies eligible for meta-analysis (see Gerstner et al., 2017) that met the following inclusion criteria: (i) conducted in agroforestry systems dominated or subdominated by an oak tree species; (ii) addressing the effects of livestock; (iii) comprising both livestock grazed and ungrazed (control) treatments; (iv) investigating the effects on early tree life stages, including seeds, seedlings, or saplings; (v) and whose response variables included measurements of acorn survival, seedling and/or sapling survival, seedling growth, and seedling density.

To supplement the search, we thoroughly examined the reference lists of each retained article, which resulted in the inclusion of the following publications not captured by the initial search string criteria: Allred et al., 2012; Laskurain et al., 2013; and Pearse et al., 2014. In total, our search identified 54 case studies from 29 scientific articles that fulfilled the specified criteria.

2.2. Data extraction

We extracted the sample size, and then the mean and the standard deviation of the response variables per treatment from text, tables, or graphs. When not provided in the text or tables, we extracted values from graphs by zooming in on the screen. Survivals of seeds, seedlings, or saplings were expressed as percentages, calculated as (subjects at end ÷ initial subjects) × 100 if not directly provided. When not directly provided by the authors, we derived growth as the variation in height over time, and density as the number of individuals per square meter. We relied on the authors' definitions to differentiate between seedlings and saplings of the same species, acknowledging minor variations in this classification across studies. When the included studies involved multiple levels of grazing treatment (e.g., Rossetti and Begella, 2014; Dorji et al., 2020), we calculated an average where applicable. To compare the effects of livestock in different oak agroforestry systems, we categorized each case study into two types: (1) oaks and (2) oaks with broadleaves and/or conifers. To compare livestock effects by animal size, we categorized the study cases as either large (cattle, horses), small (sheep, goats), or mixed. Thus, a case study in our meta-analysis was defined as a unique combination of agroforestry type (oaks, oaks with broadleaves and/or conifers), livestock size (small, mixed, large), life stage (acorn, seedling, sapling), and response variable (survival, growth, density).

Among 29 scientific articles (Table 1), 12 featured one case study, 12 contained two, and 2 included three. Three articles (Rossetti and Begella, 2014; Costa et al., 2017; and Murphy et al., 2021) each contributed four case studies, which raises potential issues of pseudo-replication across a total of 54 case studies (Massad and Dyer, 2010). In some instances, we combined results from different time periods (years, months) presented separately in the study, if the data were collected in the same study areas.

2.3. Analyses

For each of the 54 study cases, we used Hedges' *d* metric and a confidence interval (CI) to estimate effect sizes (Hedges, 1981; Gurevitch and Hedges, 2001). The analyses were performed using the *metafor* package (version 3.8-1; Viechtbauer, 2010) in R (version 4.2.2; R Core Team, 2020). Hedges' *d* represents the standardized mean difference between areas with and without livestock. Negative values indicate lower survival for acorns, seedlings, and saplings, as well as reduced seedling growth and sapling density in grazed areas compared to control areas. Positive values indicate the opposite. We considered an effect size as significant if its 95% CI did not overlap with zero (Koricheva et al., 2013). Effect sizes are commonly interpreted using Cohen (1988)'s criteria: <|0.2| is low, |0.2–0.5| is moderate, >|0.8| is high, and >1.0 is very high. To account for potential pseudo-replication and dependencies among case studies reported within the same study, we used the *robust* function from the *metafor* package, which provides robust variance estimates when multiple effect sizes are derived from the same article (Hedges et al., 2010).

We used random-effects meta-analyses to estimate mean effect sizes across pools of case studies. This approach assumes that the effect sizes in case studies are a random sample of all possible effect sizes (Borenstein et al., 2010). First, we estimated the grand mean effect size and 95% CI across all studies to see if livestock had a general effect on all the response variables combined (Koricheva et al., 2013). Then, to measure the consistency across studies, we calculated the among-studies heterogeneity (τ^2 and associated Q statistics). To account for the dependence of τ^2 on sample size, we also calculated I^2, a standardized estimate of total heterogeneity ranging from 0 to 1 (Nakagawa et al., 2017; Borenstein, 2022). To assess whether there was evidence of an overall effect of livestock on a particular group of response variables (e.g., survival,

combining all the early tree life stages), we calculated omnibus tests (e.g., Moreira et al., 2019). Last, we assessed publication bias (Appendix A) using funnel plots (Fig. A.1, Appendix A) and Rosenthal's fail-safe numbers (Koricheva et al., 2013). Publication bias is a critical concern in meta-analysis, as studies with statistically significant results are often more likely to be published than those with nonsignificant findings (Fragkos et al., 2014).

3. Results

3.1. Overview of the case studies

Most case studies eligible for meta-analysis were conducted in Europe (n = 37), followed by the Americas (12), Asia (4), and Africa (1) (Fig. B.1, Appendix B). Eleven of the 54 case studies were carried out in the USA. Spain recorded the highest number of cases in Europe (22). The 54 case studies were extracted from peer-reviewed articles published in 22 JCR-listed journals. Among them, 10 ranked in Q1, 12 in Q2, and 5 in Q3 quartile within JCR subject categories. Nearly half of the case studies (44%) assessed the effects of mixed-size livestock, often including cattle and sheep (67% of mixed-size studies) or a combination of cattle, sheep, and goats (12%), with some featuring horses, sheep, and goats (21%). In the 39% of small-sized livestock studies, 52% examined only sheep, 9% only goats, and 38% both sheep and goats. All the large-sized livestock case studies (17%) involved cattle. Seedlings were the most common oak life stage in the case studies (48%), followed by acorns and saplings (26% each). Forty-four percent of the studies measured livestock effects on the survival of early life stages (acorn, seedling, or sapling), while 31% and 24% assessed density and growth in seedlings and saplings, respectively. Forty-eight of the 54 case studies focused on oak agroforestry systems and six included oaks with broadleaves and/or conifers.

3.2. Combined survival, growth, and density effects

Livestock had a combined negative impact on the early life stages of oaks in agroforestry systems, as measured by survival of acorns, seedlings, and saplings, and density and growth of seedlings and saplings (Fig. 2; Fig. B.2, Appendix B). The combined effect size, as represented by Hedge's *d*, was -0.87 (95% CI: [-1.12, -0.62]), indicating a high negative effect. The effect was negative, regardless of continent or country. The global meta-analysis showed a substantial amount of total heterogeneity ($\tau^2 = 0.73$, $Q_T = 4260.8$, $P < 0.001$), 98% of which was attributable to between-study heterogeneity ($I^2 = 98\%$).

3.2.1. Effects by oak early life stage

Livestock had a consistently negative impact on oak regeneration across all stages: acorn ($Q = 3008$, $P < 0.001$), seedling ($Q = 404$, $P < 0.001$), and sapling ($Q = 505$, $P < 0.001$). The effect was not deemed significantly different among these life stages ($Q_M = 2.8$, $P = 0.249$) but it uniquely reached 'very high' severity on saplings (Cohen, 1988). Variability between studies was relatively high in all three stages ($\tau^2 > 0.43$ in each case), with over 90% of this variability attributed to differences between case studies within each stage.

3.2.2. Effects by livestock size

Livestock effects varied significantly by size ($Q_M = 11.92$, P = 0.001), but were negative across categories (Fig. 3a; Fig. B.3, Appendix B). The most pronounced negative effect was observed with small-sized livestock (-1.37; [-1.81, -0.92]). In comparison, large-sized and mixed-sized livestock systems tended to exhibit less negative effects ($Z = 1.8$, $P < 0.072$ and $Z = 3.4$, $P < 0.001$, respectively). The mixed-size livestock subgroup showed lower heterogeneity in effect sizes ($\tau^2 = 0.26$) and more

than 97% of the variability was due to differences between case studies in all size subgroups.

3.2.3. Effects by oak agroforestry type

The effects of livestock did not vary between case studies carried out in agroforestry systems with oaks only and systems with oaks and broadleaves and/or conifers (Q_M = 0.03, P = 0.857) (Fig. 3b). The effects were significantly negative in both the first (Q = 33, P < 0.001) and second types of system (Q = 87, P < 0.001). In both types, substantial heterogeneity in effect sizes was observed (τ^2 > 0.71), with over 98% of the variability in effect sizes within each type attributable to between-study differences.

3.3. Effects by type of response to livestock

3.3.1. Effects on early oak survival

Of the 25 case studies examining the impact of livestock on early oak survival in agroforestry systems, an overall negative effect was found (-0.57; [-0.94, -0.19]), without dependence on the life stage (Q_M = 1.6, P = 0.459). However, the negative effect was less pronounced at the seedling stage (-0.22; [-0.82, 0.38]) and was observed in the only two case studies concerning the oak sapling stage (-0.83; [-1.37, -0.28]). The 14 case studies focusing on acorn survival provided clear evidence of a negative effect (-0.72; [-1.25, -0.18]), with 5 involving small-sized and 9 involving mixed-size livestock. Further analysis demonstrated that the impact on acorn survival was significantly more negative in case studies with small-sized livestock compared to those with mixed-size livestock (Q_M = 11.5, P < 0.001) (Fig. 4; Fig. B.4, Appendix B).

3.3.2. Effects on oak seedling and sapling growth

Among the 13 case studies examining the impact of livestock on oak seedling and sapling growth, a very high negative effect was observed (-1.36; [-1.79, -0.94]). Importantly, this effect was not influenced by the early life stage of the oaks (Q_M = 0.002, P = 0.964) or the size of the livestock (Q_M = 0.370, P = 0.831).

3.3.3. Effects on oak seedling and sapling density

The 17 case studies assessing livestock's impact on early oak density consistently revealed a negative effect (-1.01; [-1.41, -0.62]). This effect was not deemed related to the oak's life stage (Q_M = 0.023, P = 0.879) but was dependent on livestock size (Q_M = 8.038, P = 0.018). Case studies involving small-sized livestock exhibited the most pronounced negative effect on plant density (-1.47; [-2.05, -0.89]), significantly differing from those involving mixed-sized livestock (Z = -2.8, P = 0.006) (Fig. 4; Fig. B.5, Appendix B).

4. Discussion

Our meta-analysis pioneers the assessment of domestic livestock impacts on early oak life stages in global *Quercus*-dominated agroforestry systems. This is the first meta-analysis to differentiate the effects of livestock body size on the survival of acorns, seedlings, and saplings, as well as the density and growth of oak seedlings and saplings. Drawing upon a synthesis of 54 case studies conducted in diverse regions across Europe, America, Asia, and North Africa, our findings reveal an expected negative effect of livestock on oak regeneration across all life stages. However, we observed heterogeneity in the effect sizes among the studies, suggesting that factors beyond merely the presence or absence of livestock likely contribute to these variations. The overall effect size, quantified using Hedge's *d*, substantiates the significance of the endeavor, with an effect size of -0.87 (95% CI: [-1.12, -0.62]). Our results contribute to

a better understanding of the oak regeneration issues involved in silvopastoral systems across the globe.

4.1. Effects on early oak life stages

Our synthesis reveals that livestock affects negatively oak regeneration at the early developmental stages, encompassing acorns, seedlings, and saplings. For acorns, this is consistent with Leal et al. (2022), who emphasized the greater impact of wild ungulates on their survival compared to domestic livestock in Mediterranean woodlands. Our study did not examine interactions with wild ungulates or other acorn predators such as rodents and birds, which may have contributed to the observed variability in the effect on acorns across the case studies. While wild ungulates, including wild boar (Gómez and Hódar, 2008; Arosa et al., 2015) and deer (Weckerly, 2004), generally consume more acorns than domestic livestock, apart from pigs, the latter also partake in acorn consumption (Leiva and Fernández-Alés, 2003; Froutan et al., 2015; Mekki et al., 2019). Furthermore, the presence of cattle also influences rodent-mediated acorn predation and dispersal patterns (Muñoz and Bonal, 2007; Vaz et al., 2024).

The overall impact of livestock on oak seedlings, though similar in mean effect size to that on acorns, exhibited great variability across 29 case studies. This included four case studies where livestock had a positive effect. Although most studies indicated higher seedling survival in grazing-excluded areas compared to grazed areas, grazing may generate new ecological niches and enhance seedling survival (e.g., Etchebarne et al., 2016; Moradi et al., 2021), which may explain some positive effects. Also, enhanced seedling survival due to reduced competition from grasses, as a result of livestock grazing, can be an indirect positive effect of livestock presence. Additionally, oak seedlings may resprout in response to livestock browsing (Zhang et al., 2019; Vaz et al.,

2019), though their sprouting ability can vary with livestock management practices and stocking rates (Pulido et al., 2010), oak species (Fortuny et al., 2020), and local environmental conditions (Jones, 2000; Plieninger et al., 2004). Broadly, the effects of livestock depend on the recruitment niche of each oak species, which is generally conditioned by the climate and the local environment. In Mediterranean oaks, recruitment tends to be promoted under shrub cover, which helps to overcome severe summer droughts. In agroforestry ecosystems with deciduous oaks (e.g., *Quercus robur*), the clearing of shrubs by livestock can create a suitable regeneration site for light-demanding seedlings, for which there is less risk of desiccation during the summer.

Our synthesis uniquely distinguishes livestock impacts on oak seedlings and saplings, unveiling a 'very high' negative impact on saplings (Cohen, 1988). Livestock foraging and trampling not only lead to reduced sapling height but also compact the soil and deplete moisture and organic matter, adversely impacting their establishment (Laskurain et al., 2013; Moradi et al., 2021). Yet, seedling and sapling establishment may also be facilitated by nurse shrubs, namely legume species (Gómez-Aparicio et al., 2004). In such cases, if browsers feed preferentially on nurse shrubs, oak regeneration may be negatively affected. On the other hand, if shrub cover is predominantly competitive, then clearing or even browsing of competitive shrubs may contribute to regeneration (Caldeira et al., 2014). Additionally, while early tree growth benefits from the facilitation of nurse plants and microclimatic amelioration, recurring shrub-clearing for grazing creates an ever-changing microhabitat that hinders sapling growth (Gómez-Aparicio et al., 2008), and saplings with limited defenses may become preferred forage for livestock (Göldel et al., 2016).

4.2. Impact of livestock body size and foraging behaviors

Our 54 case studies reveal that livestock body size, ranging from smaller animals like sheep to larger ones like cattle, can significantly affect the early oak life stages in agroforestry systems. Studies indicate that small-sized livestock, particularly sheep and to a lesser extent goats (notably, only two case studies exclusively involve goats), have more detrimental effects on oak regeneration, from acorns to saplings, compared to those focusing on large-sized livestock. Yet, no studies specifically addressed acorn predation by large livestock. Conversely, our results reveal lower negative effects on oak regeneration in mixed grazing systems. Notably, these trends are stark in acorn survival, with smaller ruminants appearing more acorn-predatory compared to mixed grazing systems. Sheep compromise seedlings by browsing and, under high grazing pressures, by trampling, which leads to bare soil as they remove litter or moss (Laskurain et al., 2013; Rossetti and Bagella, 2014). Seasonal grazing variations, notably in Mediterranean climates, further modulate these impacts, with small ruminants often targeting oak seedlings and saplings when grass is scarce (Ferreira et al., 2013). Contrarily, cattle and equines are typically managed to graze during periods of abundant grass, such as spring (Menard et al., 2002; Celaya et al., 2007). This distinction aligns with our data, where studies on small-sized livestock indicated more pronounced negative effects on oak seedling and sapling densities than those on mixed-size livestock. However, factors like soil compaction, potentially more severe with cattle than sheep or goats, were not analyzed in our synthesis (Lai and Kumar, 2020).

Our meta-analysis shows that systems with mixed-size livestock in oak agroforestry systems are associated with reduced negative impacts on early oak stages, compared to systems with only small-sized or, to a lesser extent, large livestock. Previous related research has also shown that mixed-size livestock more effectively control shrub encroachment (e.g., Ferreira et al., 2013). In Sudan and Oman, small livestock like

sheep and goats were found to be more harmful to young trees than mixed-size groups and larger livestock (Ball and Tzanopoulos, 2020; Mohammed et al., 2021). Mixed-size livestock also enhance biodiversity by promoting vegetation structural complexity, benefiting a wide variety of herbaceous and arthropod species (García et al., 2013). Moreover, maintaining a variety of animal sizes and foraging behaviors also offers greater economic flexibility to farms (Anderson et al., 2012).

The lessened impact in mixed-size livestock systems may be attributed to the specific animal combinations in our data. Nearly 70% of the mixed-size case studies exclusively involved cattle and sheep. Although both are grazers, their distinct foraging behaviors, stemming from eco-physiological adaptations, can create greater vegetation heterogeneity (Adams, 1975; Hodgson et al., 1991; Benavides et al., 2009), potentially influencing oak establishment less than in areas with only sheep. While cattle, with their mobile tongues and broad, flat muzzles, are less efficient in grazing short swards, sheep, possessing smaller mouths and longer, narrower muzzles, can take smaller, more selective bites (Hofmann, 1989; Vallentine, 2001; Gordon and Benvenutti, 2006). Yet, both cattle and sheep graze on the delicate leaves of oak seedlings and saplings. The remaining case studies within this mixed-size subgroup were split between combinations of cattle, sheep, and goats, and those involving horses, sheep, and goats, suggesting that the more intense impact of goats on acorn consumption and browsing of seedlings and saplings is moderated in these mixed-size arrangements. As for horses, although they are not ruminants like cattle, both species have a significant degree of grazing overlap (Ferreira et al., 2013), with similar grazing selectivity, although horses, with teeth pointing slightly forward, can graze closer to the ground. Horses and cattle also generally prefer flatter terrain compared to small ruminants (Catorci et al., 2012), making acorns and young oaks on slopes less vulnerable to these larger animals.

4.3. Implications for oak conservation and management

Our meta-analysis reveals that livestock generally have a negative impact on oak regeneration, though effects vary by body size and are less pronounced in mixed-body-size grazing systems. Our findings challenge the view by a few authors that replacing cattle with sheep is less harmful to young plants (e.g., López-Sánchez et al., 2016), revealing a more complex scenario. This complexity may partly stem from the underestimation of small livestock's effects on acorns and the lack of specific studies on large livestock's acorn predation. Our synthesis highlights the significant negative effect of small livestock, particularly sheep and goats, on acorn survival when compared to mixed grazing systems. To enhance oak regeneration, adopting measures such as the individual protection of saplings and creating fenced areas during acorn shedding, germination, and early growth seasons is crucial for reducing acorn over-predation and promoting survival and early growth (Vaz et al., 2019; Löf et al., 2021). While these strategies may reflect common management practices in some well-managed forest systems, our results underscore the importance of their effective application. Yet, any exclusion activities should balance with the essential role of livestock as a source of income in these systems (Moradi et al., 2021). On the other hand, attributing larger livestock size with greater impact may arise from conflating size with related management factors. Practices often linked with larger cattle, such as mechanical mobilization for larger grazing areas, more pronounced trampling, and potentially more impactful overgrazing, could be contributing to perceived size-related effects (Pinto-Correia and Azeda, 2017).

A mixture of grazers of various sizes, such as sheep and cattle, during peak grass availability can be an effective compromise for reduced competition with oak seedlings. However, applying this approach globally requires careful consideration due to limited

data from regions like Asia and northern Africa. In some Euro-Mediterranean regions, a shift to mono-specific herds favoring cattle (Catorci et al., 2012) contrasts with our results, which suggest benefits of mixed-body-size grazing systems. Conversely, management practices like rotational grazing (Plieninger et al., 2003) and stimulating livestock movement throughout the property (López-Sánchez et al., 2014), contribute significantly to sustainable oak regeneration. Traditional practices such as transhumance (Moreno and Pulido, 2009; Carmona et al., 2013) might not always fit modern contexts. Moreover, it is important to consider how livestock size and foraging behaviors interact with climatic conditions, including drought, for oak recruitment (Köchy et al., 2008). Stocking rates also influence this process and should be kept at low to intermediate levels to reduce negative impacts (López-Sánchez et al., 2014).

The heterogeneity detected in the effect sizes across studies examining the impacts of livestock on oak regeneration underscores the complexity of these effects. Crucially, livestock density plays a decisive role (see McEvoy et al., 2006), regardless of livestock type or size. For instance, a lower density of goats and sheep is likely less detrimental to oak regeneration compared to a very high density of cattle. Additionally, numerous factors such as breed type, livestock age, alternative forage, timing and duration of grazing, and the level of adaptation to young trees also significantly influence grazing impacts (Öllerer et al., 2019). These variables go beyond the simple presence or absence of livestock, which is a common element in all studies included in this meta-analysis, and they may contribute to the observed variability in effects.

4.4. Future research directions

Our analysis highlights imbalances in livestock impact studies eligible for meta-analysis on oak regeneration. Density research predominantly covers seedlings, with

sapling studies being limited. Conversely, sapling growth is slightly more examined than seedling growth. Although acorn survival is relatively well-researched, the specific impacts of large livestock like cattle are overlooked. This indicates a need for broader research across oak life stages.

The scarcity of studies in certain regions corresponds to a gap in understanding the effects of varied domestic livestock. The limited focus on goats and the absence of other livestock in our synthesis are surprising, apart from cattle, horses, and sheep. Furthermore, all studies addressing the effects of larger livestock have exclusively examined cattle. This highlights a need for broader, more inclusive research to encompass a wider range of domestic livestock and their impacts on oak agroforestry systems.

5. Conclusions

This meta-analysis evaluates livestock impacts on oak regeneration in *Quercus*-dominated agroforestry, distinguishing effects on acorns, seedlings, and saplings. Our findings show a high negative effect on early oak life stages linked to livestock size and foraging behaviors. Mixed-size systems mitigate these impacts better than single-size (especially small) livestock systems, as smaller livestock like sheep and goats particularly negatively impact acorn survival and seedling/sapling density. Our analysis challenges the idea that replacing cattle with sheep is less harmful to early oak stages, revealing the underappreciated impact of smaller livestock on acorn survival. Oak regeneration strategies should continue to employ established measures such as sapling protection in well-managed systems. Additionally, integrating livestock of diverse sizes and foraging behaviors, as well as establishing livestock-excluded areas during acorn seasons, can further enhance these practices and improve outcomes. Our synthesis urges

the importance of expanded research in diverse regions and on varied livestock to refine agroforestry management globally.

Authors' contributions

Abdullah Wadud: Investigation, Formal analysis, Writing - Original Draft **Miguel Bugalho:** Writing - Review & Editing, Supervision **Pedro Vaz:** Conceptualization, Formal analysis, Writing - Original Draft, Writing - Review & Editing, Supervision.

Acknowledgments

We acknowledge the researchers whose data supported this meta-analysis. AIW (PT/BD/143139/2018; SUSFOR—Sustainable Forests and Products Doctoral Program PD.00157.2012; CEABN-InBIO DOI 10.54499/UIDB/50027/2020; InBIO DOI 10.54499/LA/P/0048/2020) and PGV (SFRH/BPD/105632/2015; cE3c DOI 10.54499/UIDB/00329/2020; CHANGE DOI 10.54499/LA/P/0121/2020) were funded by FCT—Portuguese Science and Technology Foundation. We are deeply grateful for the valuable suggestions from three anonymous reviewers.

References

Abraham, E. M., Sklavou, P., Loufi, A., Parissi, Z. M., Kyriazopoulos, A. P., 2018. The effect of combined herbivory by wild boar and small Ruminants on the regeneration of a deciduous oak forest. Forests, 9, 580. https://doi.org/10.3390/f9090580.

Acácio, V., Holmgren, M., Moreira, F., Mohren, G.M.J. 2010. Oak persistence in Mediterranean landscapes: the combined role of management, topography, and wildfires. Ecology and Society, 15, 40. http://www.ecologyandsociety.org/vol15/iss4/art40.

Adams, S.N. 1975. Sheep and cattle grazing in forests - review. Journal of Applied Ecology, 12, 143–152. https://doi.org/10.2307/2401724.

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.

Allred, B. W., Fuhlendorf, S. D., Smeins, E. F., Taylo, C. A. 2012. Herbivore species and grazing intensity regulate community composition and an encroaching woody plant in semi-arid rangeland. Basic and Applied Ecology, 13, 149–158. https://doi.org/10.1016/j.baae.2012.02.007.

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.

Anderson, D.M., Fredrickson, E.L., Estell, R.E. 2012. Managing livestock using animal behavior: mixed-species stocking and flerds. Animal, 6, 1339–1349. https://doi.org/10.1017/s175173111200016x.

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.

Ball, L., Tzanopoulos, J. 2020. Livestock browsing affects the species composition and structure of cloud forest in the Dhofar Mountains of Oman. Applied Vegetation Science, 23, 363–376. https://doi.org/10.1111/avsc.12493.

Benavides, R., Celaya, R., Ferreira, L.M.M., Jáuregui, B.M., García, U., Osoro, K. 2009. Grazing behaviour of domestic ruminants according to flock type and subsequent vegetation changes on partially improved heathlands. Spanish Journal of Agricultural Research, 7, 417–430. https://doi.org/10.5424/sjar/2009072-432.

Bobiec, A., Reif, A., Öllerer, K. 2018. Seeing the oakscape beyond the forest: a landscape approach to the oak regeneration in Europe. Landscape Ecology, 33, 513-528. https://doi.org/10.1007/s10980-018-0619-y.

Borenstein, M., Hedges, L.V., Higgins, J.P.T., Rothstein, H.R. 2010. A basic introduction to fixed-effect and random-effects models for meta-analysis. Research Synthesis Methods, 1, 97–111. https://doi.org/10.1002/jrsm.12.

Borenstein. M. 2022. In a meta-analysis, the I-squared statistic does not tell us how much the effect size varies. Journal of Clinical Epidemiology, 152, 281–284. https://doi.org/10.1016/j.jclinepi.2022.10.003.

Branco, M., Branco, C., Merouani, H., Almeida, M.H. 2002. Germination success, survival and seedling vigour of *Quercus suber* acorns in relation to insect damage. Forest Ecology and Management, 166, 159–164. https://doi.org/10.1016/S0378-1127(01)00669-7.

Branco, M., Ramos, P.A. 2009. Coping with pest and diseases, in: Aronson, J., Pereira, J.S., Pausas, J.G. (Eds.), Cork Oak Woodlands on the Edge. ISLANDPRESS, Washington, London, pp. 103–112.

Brasier, C.M. 1992. Oak tree mortality in Iberia. Nature, 360, 539–539. https://doi.org/10.1038/360539a0.

Brasier, C.M. 1996. *Phytophthora cinnamomi* and oak decline in southern Europe. Environmental constraints including climate change. Annales des Sciences Forestieres, 53, 347–358. https://doi.org/10.1051/forest:19960217.

Brown, S.E., Miller, D.C., Ordonez, P.J., Baylis, K. 2018. Evidence for the impacts of agroforestry on agricultural productivity, ecosystem services, and human well-being in high-income countries: a systematic map protocol. Environmental Evidence, 7. https://doi.org/10.1186/s13750-018-0136-0.

Bugalho, M.N., Milne, J.A., Racey, P.A. 2001. The foraging ecology of red deer (*Cervus elaphus*) in a Mediterranean environment: is a larger body size advantageous? Journal of Zoology, 255, 285–289. https://doi.org/10.1017/S0952836901001376.

Bugalho, M.N., Plieninger, T., Aronson J., Ellatifi, M., Crespo, D.G. 2009. Open woodlands: a diversity of uses (and overuses). In: Aronson, J., Pereira, J.S., Pausas, J. (Eds) Cork ak Woodlands on the Edge: Ecology, biogeography, and restoration of an ancient Mediterranean ecosystem (pp: 33–45). Island Press, Washington DC.

Bugalho, M.N., Caldeira, M.C., Pereira, J.S., Aronson, J., Pausas, J.G. 2011. Mediterranean cork oak savannas require human use to sustain biodiversity and ecosystem services. Frontiers in Ecology and the Environment. 9, 278–286. https://doi.org/10.1890/100084.

Caldeira, M.C., Ibáñez, I., Nogueira, C., Bugalho, M.N., Lecomte, X., Moreira, A., Pereira, J.S. 2014. Direct and indirect effects of tree canopy facilitation in the recruitment of Mediterranean oaks. Journal of Applied Ecology, 51, 349–358. https://doi.org/10.1111/1365-2664.12189.

Canelo, T., Pérez-Izquierdo, C., Gaytán, A., Bonal, R. 2021. Intraguild predation of weevils by livestock reduces acorn pests in oak silvopastoral systems. Journal of Pest Science, 94, 541–551. https://doi.org/10.1007/s10340-020-01278-8.

Carmona, C. P., 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. https://doi.org/10.1016/j.biocon.2012.11.015.

Catorci, A., Gatti, R., Cesaretti, S. 2012. Effect of sheep and horse grazing on species and functional composition of sub-Mediterranean grasslands. Applied Vegetation Science, 15, 459–469. https://doi.org/10.1111/j.1654-109X.2012.01197.x.

Celaya, R., Oliván, M., Ferreira, L.M.M., Martínez, A., García, U., Osoro, K. 2007. Comparison of grazing behaviour, dietary overlap and performance in non-lactating domestic ruminants grazing on marginal heathland areas. Livestock Science, 106, 271–281. https://doi.org/10.1016/j.livsci.2006.08.013.

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

Clements, David R., Luginbill, Seth, Jordan, David A., Dragt, Randall Van, and Pelant, Robert K. 2011. Techniques to promote Garry Oak seedling growth and survival in areas with high levels of herbivory and competition. Northwest Science, 85, 172–181. https://doi.org/10.3955/046.085.0208.

Cohen, J. 1988. Statistical Power Analysis for the Behavioral Sciences (2nd ed.). Hillsdale, NJ: Lawrence Erlbaum Associates, Publishers.

Campos, P., Daly-Hassen, H., Ovando, P., 2007. Cork oak forest management in Spain and Tunisia: two case studies of conflicts between sustainability and private income. International Forestry Review 9, 610–626. https://doi.org/10.1505/ifor.9.2.610.

Costa, A., Villa, S., Alonso, P., García-Rodríguez, J.A., Martíin, F.J., Martínez-Ruiz, C., Fernández-Santos, B. 2017. Can native shrubs facilitate the early establishment of contrasted co-occurring oaks in Mediterranean grazed areas? Journal of Vegetation Science, 28, 1047–1056. https://doi.org/10.1111/jvs.12550.

Cushman, J.H., Saunders, L.E., Refsland, T.K. 2020. Long-term and interactive effects of different mammalian consumers on growth, survival, and recruitment of dominant tree species. Ecology and Evolution, 10, 8801–8814. https://doi.org/10.1002/ece3.6578.

Davis, F. W., Tyler, C. M., Mahall, B. E. 2011. Consumer control of oak demography in a Mediterranean-climate savanna. Ecosphere 2, 1–21. https://doi.org/10.1890/es11-00187.1

Díaz, M., Sánchez-Mejía, T., Morán-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.

Díaz-Hernández, R., Villardón, V.L.J., Martínez-Ruiz, C., Fernández-Santos, B. 2021. The effects of native shrub, fencing, and acorn size on the emergence of contrasting co-occurring oak in Mediterranean grazed areas. Forests, 12, 2–14. https://doi.org/10.3390/f12030307.

Dorji, T., Facelli, J. M., Norbu, T., Delean, S., Brookes, J. D. 2020. Tree shelters facilitate brown oak seedling survival and establishment in a grazing-dominant forest of Bhutan, Eastern Himalaya. Restoration Ecology, 28, 1145–1157. https://doi.org/10.1111/rec.13176.

Dufour-Dror, J.M. 2007. Influence of cattle grazing on the density of oak seedlings and saplings in a Tabor oak forest in Israel. Acta Oecologica, 31, 223–228. https://doi.org/10.1016/j.actao.2006.11.003.

Espelta, J. M., Habrouk, A., Retana, J. 2006. Response to natural and simulated browsing of two Mediterranean oaks with contrasting leaf habit after a wildfire. Ann. For. Sci. 63, 441–447. https://doi.org/10.1051/forest:2006024.

Etchebarne, V., Brazeiro, A. 2016. Effects of livestock exclusion in forests of Uruguay: Soil condition and tree regeneration. Forest Ecology and Management, 362, 120–129. http://dx.doi.org/10.1016/j.foreco.2015.11.042.

FAO. 2023. The state of food and agriculture 2023 – Revealing the true cost of food to transform agrifood systems. Rome. https://doi.org/10.4060/cc7724en

Ferreira, L.M.M., Celaya, R., Benavides, R., Jáuregui, B.M., García, U., Santos, A.S., García, R.R., Rodrigues, M.A.M., Osoro, K. 2013. Foraging behaviour of domestic herbivore species grazing on heathlands associated with improved pasture areas. Livestock Science, 155, 373–383. http://dx.doi.org/10.1016/j.livsci.2013.05.007.

Fortuny, X., Carcaillet, C., Chauchard, S. 2020. Selective and taxon-dependent effects of semi-feral cattle grazing on tree regeneration in an old-growth Mediterranean mountain forest. Forest Ecosystems, 7. https://doi.org/10.1186/s40663-020-00222-7.

Fragkos, C. K., Tsagris. M., Frangos. C. C. 2014. Publication Bias in Meta-Analysis: Confidence Intervals for Rosenthal's Fail-Safe Number. Hindawi Publishing Corporation. International Scholarly Research Notices, 2014, 17. https://doi.org/10.1155/2014/825383.

Froutan, E., Azizi, O., Sadeghi, G., Fatehi, F., Lashkari, S. 2015. Effects of different concentrations of ground oak acorn on growth performance, blood parameters and carcass characteristics of goat kids. Animal Production Science, 55, 87–92. https://doi.org/10.1071/an13312.

Gallego, D., Morán-López, T., Torre, I., Navarro-Castilla, A., Barja, I., Díaz, M. 2017. Context dependence of acorn handling by the Algerian mouse (*Mus spretus*). Acta Oecologica, 84, 1–7. https://doi.org/10.1016/j.actao.2017.07.002.

García, R.R., Fraser, M.D., Celaya, R., Ferreira, L.M.M., García, U., Osoro, K. 2013. Grazing land management and biodiversity in the Atlantic European heathlands: a

review. Agroforestry Systems, 87, 19–43. https://doi.org/10.1007/s10457-012-9519-3.

Gerstner, K., Moreno-Mateos, D., Gurevitch, J., Beckmann, M., Kambach, S., Jones, H.P., Seppelt, R. 2017. Will your paper be used in a meta-analysis? Make the reach of your research broader and longer lasting. Methods in Ecology and Evolution, 8, 777–784. https://doi.org/10.1111/2041-210x.12758.

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

Gómez-Aparicio L., Zamora, R., Castro, J., Hódar, J.A. 2008. Facilitation of tree saplings by nurse plants: Microhabitat amelioration or protection against herbivores? Journal of Vegetation Science. 19, 161–172. https://doi.org/10.3170/2008-8-18347.

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

Gómez, J.M., García, D., Zamora, R. 2003. Impact of vertebrate acorn- and seedling-predators on a Mediterranean *Quercus pyrenaica* forest. Forest Ecology and Management 180, 125–134. https://doi.org/10.1016/s0378-1127(02)00608-4.

Gómez, J.M., Hódar, J.A. 2008. Wild boars (*Sus scrofa*) affect the recruitment rate and spatial distribution of holm oak (*Quercus ilex*). Forest Ecology and Management, 256, 1384–1389. https://doi.org/10.1016/j.foreco.2008.06.045.

González-Rodriguez, V., Villar, R. 2012. Post-dispersal seed removal in four Mediterranean oaks: species and microhabitat selection differ depending on large

herbivore activity. Ecological Research, 27, 587–594. https://doi.org/10.1007/s11284-012-0927-7.

Gordon, I.J., Benvenutti, M. 2006. Food in 3D: how ruminant livestock interact with sown sward architecture at the bite scale. Feeding in domestic vertebrates: from structure to behaviour (ed. V. Bell), pp. 263-277. CABI Wallingford UK.

Grellier, S., Barot, S., Janeau, J., Ward, D. 2012. Grass competition is more important than seed ingestion by livestock for Acacia recruitment in South Africa. Plant Ecology, 213, 899–908. https://doi.org/10.1007/s11258-012-0051-3.

Gurevitch, J., Hedges, L.V. 2001. Meta-analysis: combining the results of independent experiments. In: Scheiner SM, Gurevitch J (eds) Design and analysis of ecological experiments. Oxford University Press, New York, pp 347–369.

Harper, J.L. 1977. Population Biology of Plants. Academic Press, London.

Hedges, L.V. 1981. Distribution theory for Glass's estimator of effect size and related estimators. Journal of Educational Statistics, 6, 107–128. https://doi.org/10.2307/1164588.

Hedges, L.V., Tipton, E., Johnson, M.C. 2010. Robust variance estimation in meta-regression with dependent effect size estimates. Research Synthesis Methods, 1, 39–65. https://doi.org/10.1002/jrsm.5

Hodgson, J., Forbes, T.D.A., Armstrong, R.H., Beattie, M.M., Hunter, E.A. 1991. Comparative studies of the ingestive behaviour and herbage intake of sheep and cattle grazing indigenous hill plant communities. Journal of Applied Ecology, 28, 205–227. https://doi.org/10.2307/2404126.

Hofmann, R.R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive-system. Oecologia, 78, 443–457. https://doi.org/10.1007/bf00378733.

Humphrey, J., Gill, R., Claridge, J. 1998. Grazing as a management tool in European forest ecosystems. Technical Paper No. 025. Forestry Commission, Edinburg, UK.

Jones, A. 2000. Effects of cattle grazing on North American arid ecosystems: A quantitative review. Western North American Naturalist, 60, 155–164.

Kalbitzer U, McInnis V, Chapman C.A. 2019. Primates create seedling growth hotspots through pattern of dung deposition. African Journal of Ecology, 57, 190–197. https://doi.org/10.1111/aje.1258913652028.

Köchy, M., Mathaj, M., Jeltsch, F., Malkinson, D. 2008. Resilience of stocking capacity to changing climate in arid to Mediterranean landscapes. Regional Environmental Change, 8, 73. https://doi.org/10.1007/s10113-008-0048-6.

Koricheva, J., Gurevitch, J., Mengersen, K. 2013. Handbook of meta-analysis in ecology and evolution. Princeton University Press, Princeton, New Jersey, USA.

Lai, L.M., Kumar, S. 2020. A global meta-analysis of livestock grazing impacts on soil properties. PloS ONE, 15. https://doi.org/10.1371/journal.pone.0236638.

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

Leal, A. I., Bugalho, M. N., Palmeirim, J. M. 2022. Effects of ungulates on oak regeneration in Mediterranean Woodlands: A meta-analysis. Forest Ecology and Management, 509, 120077. https://doi.org/10.1016/j.foreco.2022.120077.

Leiva, M. J., Fernández-Alés, R. 2003. Post-dispersive losses of acorns from Mediterranean savannah-like forest and shrublands. Forest Ecology and Management, 176, 265–271. http://dx.doi.org/10.1016/S0378-1127(02)00294-3.

Leiva, M. J., Fernández-Alés, R. 2005. Holm-oak (*Quercus ilex* subsp. *Ballota*) acorns infestation by insects in Mediterranean dehesas and shrublands: Its effect on acorn germination and seedling emergence. Forest Ecology and Management, 212, 221–229. https://doi.org/10.1016/j.foreco.2005.03.036.

Leiva, M.J., Vera, M. 2015. Effect of artificial shelters of dead branches on acorn survival and dispersal in shrub-lacking Mediterranean dehesas. New Forests, 46, 965–978. https:// doi.org/10.1007/s11056-015-9486-4.

Leiva, M.J., Sobrino-Mengual, G. 2022. 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.

Löf, M., Barrere, J., Engman, M., Petersson, L.K., Villalobos, A. 2021. The influence of fencing on seedling establishment during reforestation of oak stands: a comparison of artificial and natural regeneration techniques including costs. European Journal of Forest Research, 140, 807–817. https://doi.org/10.1007/s10342-021-01369-w.

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.org/10.1371/journal.pone.0105472.

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.

Massad, T. J., Dyer, L. A. 2010. A meta-analysis of the effects of global environmental change on plant-herbivore interactions. Arthropod-Plant Interactions, 4, 181–188. https://doi.org/10.1007/s11829-010-9102-7.

Mazzini, F., Relva, M.A., Malizia, L.A. 2018. Impacts of domestic cattle on forest and woody ecosystems in southern South America. Plant Ecology, 219, 913–925. https://doi.org/10.1007/s11258-018-0846-y.

McEvoy, M. P., McAdam, J. H., 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. 66, 85–92. https://doi.org/10.1007/s10457-005-2916-0.

Mekki, I., Smeti, S., Hajji, H., Yagoubi, Y., Mahouachi, M., Atti, N. 2019. Effect of oak acorn (*Quercus ilex*) intake during suckling and fattening of Barbarine lambs on growth, meat quality and fatty acid profile. Journal of Animal and Feed Sciences, 28, 22–30. https://doi.org/10.22358/jafs/102757/2019.

Mena, Y., Ruiz-Mirazo, J., Ruiz, F.A., Castel, J.M. 2016. Characterization and typification of small ruminant farms providing fuelbreak grazing services for wildfire prevention in Andalusia (Spain). Science of the Total Environment, 544, 211–219. https://doi.org/10.1016/j.scitotenv.2015.11.088.

Menard, C., Duncan, P., Fleurance, G., Georges, J.Y., Lila, M. 2002. Comparative foraging and nutrition of horses and cattle in European wetlands. Journal of Applied Ecology, 39, 120–133. https://doi.org/10.1046/j.1365-2664.2002.00693.x.

Mohammed, E. M. I., Hammed, A. M. E., Minnick, T. J., Ndakidemi, P. A., Treydte, A. C. 2021. Livestock browsing threatens the survival of *Balanites aegyptiaca* seedlings and saplings in Dinder Biosphere Reserve, Sudan, Journal of Sustainable Forestry, 41, 1046–1063. https://doi.org/10.1080/10549811.2021.1935279.

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.

Moreira, X., Castagneyrol, B., Abdala-Roberts., Traveset, A. 2019. A meta-analysis of herbivore effects on plant attractiveness to pollinators. Ecology, 100, e02707. https://doi.org/10.1002/ecy.2707.

Moreno, G., Pulido, F.J. 2009. The functioning, management and persistence of dehesas. In: Rigueiro-Rodríguez, A., McAdam, J., Mosquera-Losada, M.R. (Eds.), Agroforestry in Europe. Current Status and Future Prospects. Springer, Dordrecht, Netherlands, pp. 127–160.

Moreno-Fernández, D., Ledo, A., Martín-Benito, D., Cañellas, I., Gea-Izquierdo, G. 2019. Negative synergistic effects of land-use legacies and climate drive widespread oak decline in evergreen Mediterranean open woodlands. Forest Ecology and Management, 432, 884–894. https://doi.org/10.1016/j.foreco.2018.10.023.

Muñoz, A., Bonal, R. 2007. Rodents change acorn dispersal behaviour in response to ungulate presence. Oikos, 116, 1631-1638. DOI:10.1111/j.2007.0030-1299.15710.x.

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.

Murphy, T. R, Hanley, M. E., Ellis, J. S., Lunt, P. H. 2021. Optimizing opportunities for oak woodland expansion into upland pastures. Ecological Solutions and Evidence, 3, e12126. https://doi.org/10.1002/2688-8319.12126.

Nixon, K.C. 2006. Global and neotropical distribution and diversity of oak (genus *Quercus*) and oak forests, in: Kappelle, M. (Eds.), Ecology and conservation of neotropical Montane Oak forests, ecological studies, Springer, Berlin, pp. 3–13.

Öllerer, K., Varga, A., Kirby, K., Demeter, L., Biró, M., Bölöni, J., Molnár, Z. 2019. Beyond the obvious impact of domestic livestock grazing on temperate forest vegetation - A global review. Biological Conservation, 237, 209–219. https://doi.org/10.1016/j.biocon.2019.07.007.

Pantera, A., Papadopoulos, A., Papanastasis, V., P. 2018. Valonia oak agroforestry systems in Greece: an overview. Agroforestry Systems, 92, 921–931. https://doi.org/10.1007/s10457-018-0220-z.

Papachristou, T.G., Platis, P.D., Nastis, A.S. 2005. Foraging behaviour of cattle and goats in oak forest stands of varying coppicing age in Northern Greece. Small Ruminant Research, 59, 181–189. https://doi.org/10.1016/j.smallrumres.2005.05.006.

Papachristou, T.G., Platis, P.D. 2011. The impact of cattle and goats grazing on vegetation in oak stands of varying coppicing age. Acta Oecologica, 37, 16–22. https://doi.org/10.1016/j.actao.2010.11.001.

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.

Pearse, I., Griswold, S., Pizarro, D., Koenig, W.D. 2014. Stage and size structure of three species of oaks in Central Coastal California. Madroño, 61, 1–8. https://doi.org/10.3120/0024-9637-61.1.1.

Phillips, R., McDougald, N. K., Atwill, E.R., McCreary, D. 2007. Exclosure size affects young blue oak seedling growth. California Agriculture, 61, 16–19.

Pinto-Correia, T., Azeda, C. 2017. Public policies creating tensions in Montado management models: Insights from farmers' representations. Land Use Policy, 64, 76–82. https://doi.org/10.1016/j.landusepol.2017.02.029.

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 Environments, 57, 345–364. https://doi.org/10.1016/S0140-1963(03)00103-4.

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.

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.

Príncipe, A., Matos, P., Sarris, D., Gaiola, G., do Rosario, L., Correia, O., Branquinho, C. 2019. In Mediterranean dry lands microclimate affects more tree seedlings than adult trees. Ecological Indicators, 106, 105476. https://doi.org/10.1016/j.ecolind.2019.105476.

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. Ecoscience, 12, 92–102. https://doi.org/10.2980/i1195-6860-12-1-92.1.

Pulido, F.J., Díaz, M., de Trucios, S.J.H. 2001. Size structure and regeneration of Spanish holm oak Quercus ilex forests and dehesas: effects of agroforestry use on their long-term sustainability. Forest Ecology and Management, 146, 1–13. https://doi.org/10.1016/S0378-1127(00)00443-6.

R Core Team, 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Reiner, R., Craig, A. 2011. Conservation easements in California blue oak woodlands: Testing the assumption of livestock grazing as a compatible use. Natural Areas Journal, 31, 408–413. https://doi.org/10.3375/043.031.0411.

Rogers, R., Johnson, P.S., Loftis, D.L., 1993. An overview of oak silviculture in the United States - The past, present and future. Annales des Sciences Forestieres 50, 535–542. https://doi.org/10.1051/forest:19930602.

Rossetti, I., Bagella, S. 2014. Mediterranean *Quercus suber* wooded grasslands risk disappearance: New evidences from Sardinia (Italy). Forest Ecology and Management, 329, 148–157. https://doi.org/10.1016/j.foreco.2014.06.010.

Rouet-Leduc, J., Pe'er, G., Moreira, F., Bonn, A., Helmer, W., Shahsavan Zadeh, S.A.A., Zizka, A., van der Plas, F. 2021. Effects of large herbivores on fire regimes and wildfire mitigation. Journal of Applied Ecology, 58, 2690–2702. https://doi.org/10.1111/1365-2664.13972.

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 of Forest Research, 50, 371–379. https://doi.org/10.1139/cjfr-2019-0181.

Ruiz-Mirazo, J., Robles, A.B. 2012. Impact of targeted sheep grazing on herbage and holm oak saplings in a silvopastoral wildfire prevention system in south-eastern Spain. Agroforestry Systems, 86, 477–491. https://doi.org/10.1007/s10457-012-9510-z.

Ruiz-Mirazo, J., Robles, A.B., González-Rebollar, J.L. 2011. Two-year evaluation of fuelbreaks grazed by livestock in the wildfire prevention program in Andalusia (Spain). Agriculture Ecosystems & Environment, 141, 13–22. https://doi.org/10.1016/j.agee.2011.02.002.

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.

Stavi, I., Thevs, N., Welp, M., Zdruli, P. 2022. Provisioning ecosystem services related with oak (*Quercus*) systems: a review of challenges and opportunities. Agroforestry Systems, 96, 293–313. https://doi.org/10.1007/s10457-021-00718-3.

Szewczyk, J., Szwagrzyk, J. 2010. Spatial and temporal variability of natural regeneration in a temperate old-growth forest. Annals of Forest Science, 67. https://doi.org/10.1051/forest/2009095.

Tantray, Y.R., Wani, M.S., Hussain, A. 2017. Genus *Quercus*: an overview. International Journal of Advance Research in Science and Engineering, 6, 1880–1886.

Taylor, C.A., Rising, J. 2021. Tipping point dynamics in global land use. Environmental Research Letters, 16, 14. https://doi.org/10.1088/1748-9326/ac3c6d.

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.

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.

Vallentine, J.F. 2001. Grazing management, 2nd ed. Academic Press, San Diego, CA.

Vandenberghe, C., Frelechoux, F., Moravie, M., Gadallah, F., Buttler, A. 2007. Short-term effects of cattle browsing on tree sapling growth in mountain wooded pastures. Plant Ecology, 188, 253–264. https://doi.org/10.1007/s11258-006-9160-1.

Varga, A., Demeter, L., Ulicsni, V., Öllerer, K., Biró, M., Babai, D., Molnár, Z. 2020. Prohibited, but still present: local and traditional knowledge about the practice and impact of forest grazing by domestic livestock in Hungary. Journal of Ethnobiology and Ethnomedicine, 16, 12. https://doi.org/10.1186/s13002-020-00397-x.

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., 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.

Vázquez, D.P. 2002. Multiple effects of introduced mammalian herbivores in a temperate forest. Biological Invasions, 4, 175–191. https://doi.org/10.1023/A:1020522923905.

Vera, F.W.M. 2000. Grazing ecology and forest history. CABI publishing.

Verdú, M., Traveset, A. 2005. Early emergence enhances plant fitness: A phylogenetically controlled meta-analysis. Ecology, 86, 1385–1394. https://doi.org/10.1890/04-1647.

Viechtbauer, W. 2010. Conducting meta-analyses in R with the *metafor* package. Journal of Statistical Software, 36, 1–48. https://doi.org/10.18637/jss.v036.i03.

Weckerly, F.W. 2004. Movement of male and female black-tailed deer foraging on acorns. Northwestern Naturalist, 85, 16–19. https://doi.org/10.1898/1051-1733(2004)085<0016:MOMAFB>2.0.CO;2

Wolański, P., Bobiec, A., Ortyl, B., Makuch-Pietraś, I., Czarnota, P., Ziobro, J., Korol, M., Havryliuk, S., Paderewski, J., Kirby, K. 2021. The importance of livestock grazing at woodland-grassland interface in the conservation of rich oakwood plant

communities in temperate Europe. Biodiversity and Conservation, 30, 741–760. https://doi.org/10.1007/s10531-021-02115-9.

Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J., García, D. 2001. Effect of browsing by ungulates on sapling growth of Scots pine in a mediterranean environment: consequences for forest regeneration. Forest Ecology and Management, 144, 33–42. https://doi.org/10.1016/S0378-1127(00)00362-5.

Zhang, Y.H., Li, J., Zhang, D.Y., Wang, Z.Y., Yi, X.F. 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. Summary of articles. Livestock: S = sheep; G = goat; C = cattle; H = horse. Oak life stage: Se = seedling; Sa = sapling; Ac = acorn. Response: De = density; Gr = Growth; Su = survival. Tree species: *Q.* = *Quercus*; other = other broadleaves and/or conifers.

Study	Country	No. cases	Livestock	Stage	Response	Tree species
Reiner & Craig 2011	USA	1	S, C	Se	De	*Q. douglasii*
Clements et al. 2011	Canada	1	S	Se	Gr	*Q. garryana*
Ruiz-Mirazo & Robles 2012	Spain	2	G	Se, Sa	Gr	*Q. ilex*
Espelta et al. 2006	Spain	2	C	Sa	Gr	*Q. ilex*, *Q. cerrioides*
Abraham et al. 2018	Greece	1	S, G	Se	De	*Q. frainetto*
Plieninger et al. 2004	Spain	2	S, G	Se	De	*Q. ilex*
DufourDror et al. 2007	Israel	1	S, G, C	Se	De	*Q. ithaburensis*
Rossetti & Bagella et al. 2012	Italy	4	S	Se	Gr, De	*Q. suber*
Leiva & FernandezAles 2003	Spain	2	S	Ac	Su	*Q. ilex*
Pulido et al. 2010	Spain	1	S	Ac	Su	*Q. ilex*
Tayler et al. 2008	USA	2	S, C	Ac	Su	*Q. lobata*, *Q. agrifolia*
Arosa et al. 2015	Portugal	2	S, C, S	Ac	Su	*Q. ilex*, *Q. suber*
Davis et al. 2011	USA	1	S, C	Ac	Su	*Q. lobata*
Cierjacks & Hensen 2004	USA	1	S, G	Ac	Su	*Q. ilex*
Leiva & Vera 2015	Spain	3	S, G, H	Ac	Su	*Q. ilex*, *Q. suber*
Allred et al. 2012	USA	2	S, G, C	Se	De	*Q. fusiformis*
Pearse et al. 2014	USA	3	S, C	Se	De	*Q. lobata*
Leiva & Sobrino-Mengual 2022	Spain	2	C	Se	Su	*Q. ilex*
Diaz-Hernandez et al. 2021	Spain	2	S, C	Ac	Su	*Q. ilex*
Parsons et al. 2021	USA	1	C	Se	De	*Q. lobata*, *Q. douglasii*, *Q. kelloggii*
Dorji et al. 2020	Bhutan	2	C	Se	Su, Gr	*Q. semecarpifolia*
Costa et al. 2017	Spain	4	S, C	Se	Su	*Q. pyrenaica*, *Q. ilex*
Murphy et al. 2021	England	4	S, G	Se, Sa	Su, Gr, De	*Q. robur*, *Q. petraea*
Roula et al. 2019	Algeria	1	S, C	Sa	Gr	*Q. suber*
Phillips et al. 2007	USA	1	S, C	Se	Gr	*Q. douglasii*
Laskurain et al. 2013	Spain	1	S	Se	Su	*Q. robur*, other
Moradi et al. 2021	Iran	1	S, G	Sa	Gr	*Q. brantii*, other
Fortuny et al. 2020	France	2	C	Se	De	*Q. pubescens*, other
Amsten et al. 2021	Sweden	2	S, G, H	Sa	Su, Gr	*Q. robur*, other

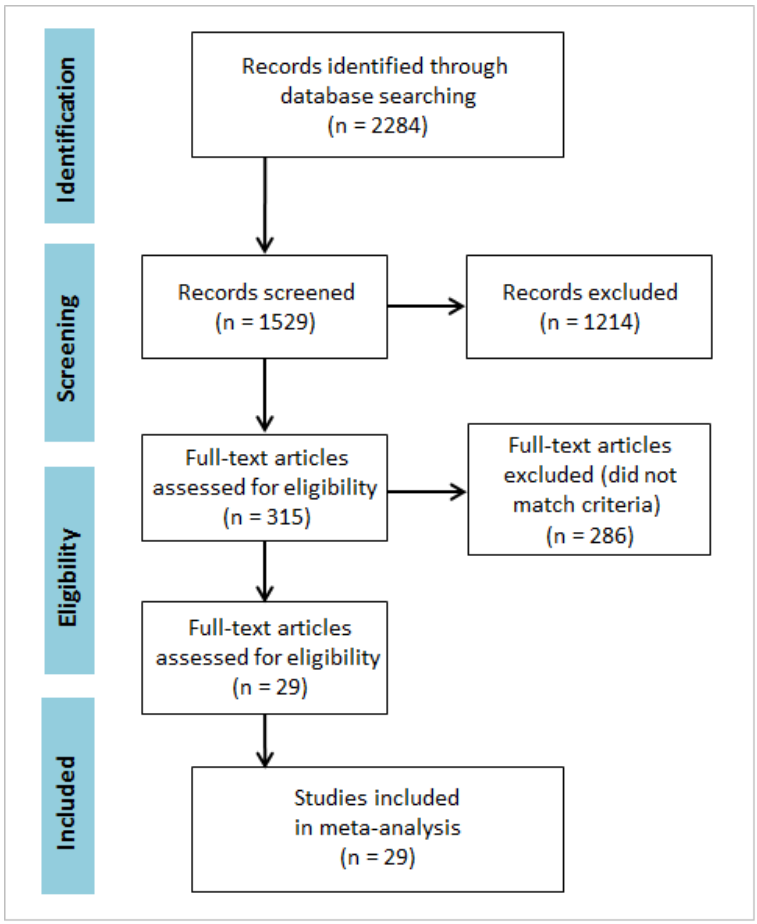

Fig. 1. PRISMA diagram illustrating the study selection process.

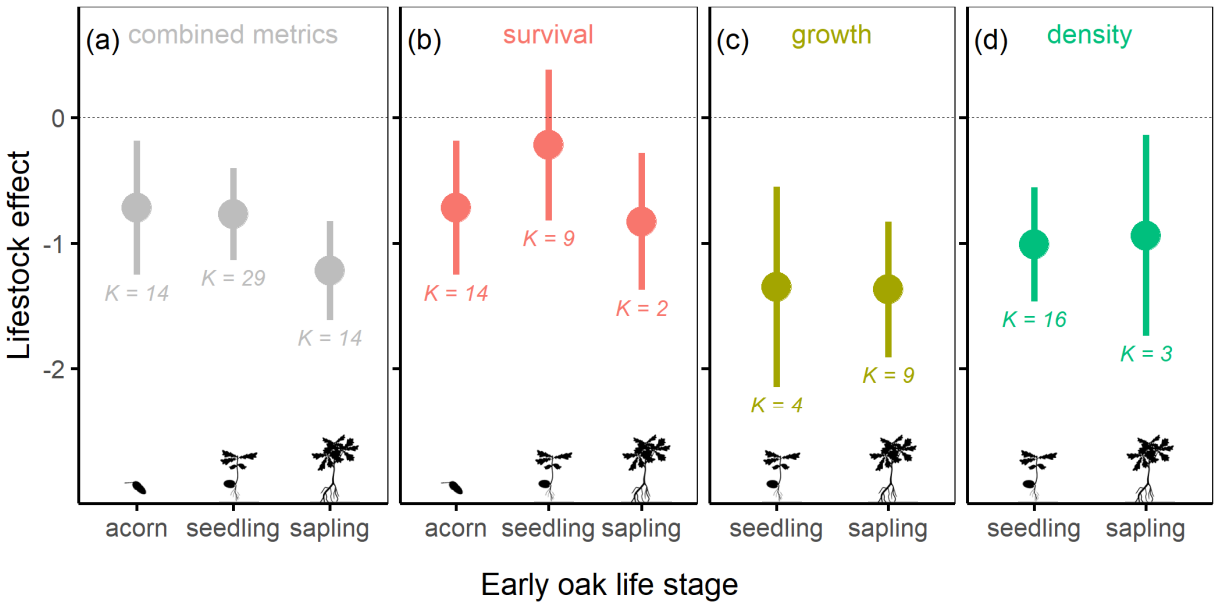

Fig. 2. Mean effect size (Hedges' *d*) of domestic livestock on combined survival, growth, and density effects across life stages (a), and on survival, growth, and density individually (b, c, d). Dots with error bars represent model parameter estimates and their 95% confidence intervals (CI). '*K*' denotes the number of case studies. The mean effect size is considered significant if the 95% CI does not intersect the dashed zero line (no effect).

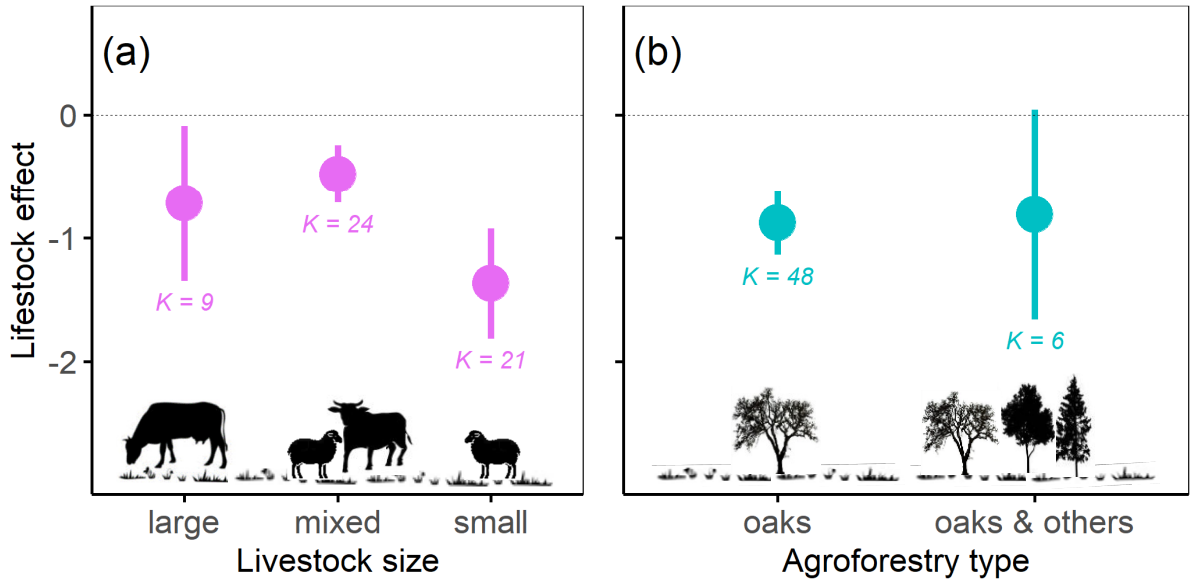

Fig. 3. Mean effect size of domestic livestock on the early life stages of oaks, categorized by body size (a) and type of agroforestry system (b; either oak trees only or oaks mixed with broadleaves and/or conifers). Refer to Figure 2 for more explanations.

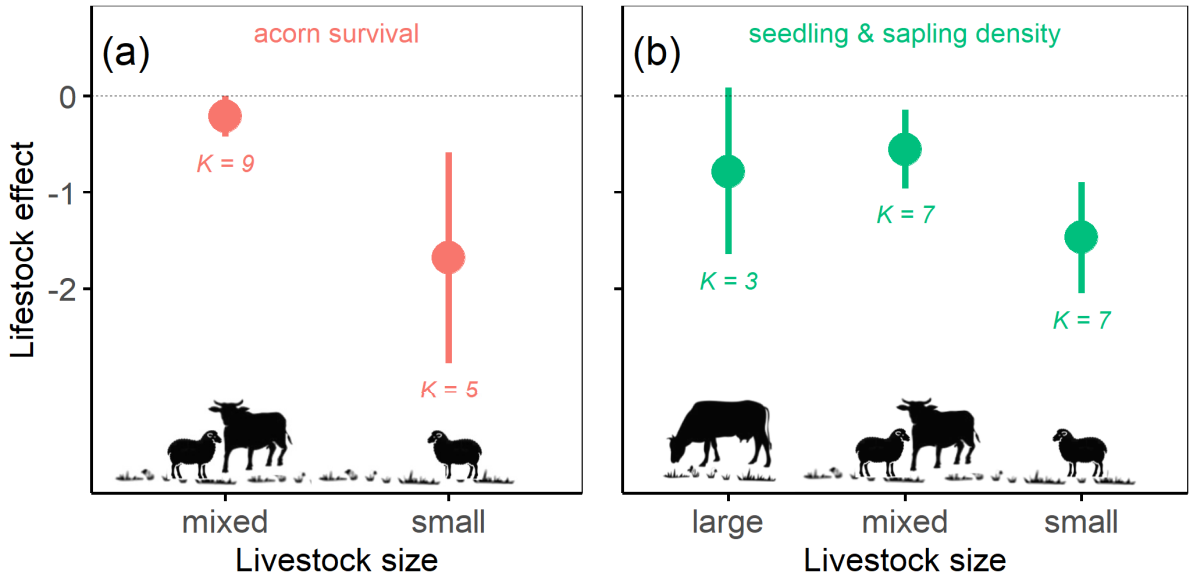

Fig. 4. Mean effect size of domestic livestock, categorized by body size, on acorn survival (a) and on seedling and sapling density (b). Refer to Figure 2 for more explanations. No study eligible for meta-analysis has analyzed the effect of large livestock on acorn survival.