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

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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 influencing the survival, growth, and density of trees' early developmental stages. To address the nuanced effects of livestock types and their size-related foraging behaviors on tree recruitment in the face of ongoing debates about their impacts, we conducted a 33-year meta-analysis in *Quercus*-dominated systems. Our analysis revealed a consistently negative effect of livestock on oak regeneration across early developmental stages—acorns, seedlings, and saplings. Significantly, livestock size influenced oak regeneration, with small-sized livestock, notably sheep and goats, having a more pronounced negative impact compared to mixed-size livestock systems. The effects of small-sized livestock were markedly detrimental on acorn survival and seedling/sapling density. Mixed-size livestock systems, often involving cows and sheep, lessen the negative effects better than single-size, especially small, livestock systems. Such findings challenge the perception of some authors that simply replacing cattle with sheep would be less harmful to oak regeneration, revealing a more complex scenario. Our results advocate for the integration of diverse livestock sizes and the consideration of protective measures, especially for acorns and saplings, to enhance oak regeneration. Future research should expand to underrepresented regions and livestock types to refine global agroforestry management practices.

Keywords: herbivory, overgrazing, 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 livestock (Allen et al., 2011). In these ecosystems, livestock of different body sizes and foraging behaviors affect key tree reproductive stages—seed, seedling, sapling—altering survival, growth, and density of new tree recruits (Pulido and Díaz, 2005). Thus, managing livestock necessitates balancing production with mitigating the grazing effects related to livestock size on each early tree life stage to ensure ecological sustainability (Brown et al., 2018). This highlights the value of aggregating insights on such effects across similar ecosystems worldwide to inform sustainable management strategies.

Among agroforestry ecosystems, *Quercus*-dominated systems are diverse, featuring Iberian dehesas and montados, North Africa's similar systems, varied practices in north-central Europe, North America's oak woodlands, and traditional oak-based agroforestry in Asia (Tantray et al., 2017). These systems span semi-natural and managed landscapes across temperate regions and are particularly valued for their economic and cultural significance (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, livestock grazing impacts, individually and across various early oak life stages, are still 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 effects (López-Sánchez et al., 2014) to positive (Leiva et al., 2022) or mixed outcomes (Laskurain et al., 2013), with livestock size being an important factor (e.g., Ball and Tzanopoulos, 2020). Overall, livestock's effect on tree regeneration—its signal and especially its magnitude—stirs ongoing debate.

Variability in livestock effects on acorn, seedling, and sapling stages, and differing metrics—survival, growth, 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 exposure, 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; Moñoz et al., 2009; Gallego et al., 2017), with oak seedlings' resilience to tissue mortality potentially mitigating grazing impacts (Zhang et al. 2019; Vaz et al. 2019). For saplings, frequent grazing and rubbing 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, and may facilitate growth by opening areas (Uytvanck et al., 2010; Reiner and Craig, 2011; Mazzini et al., 2018; Vaz et al., 2019).

Beyond an overall effect of domestic livestock, the nuances of livestock size on agroforestry regeneration warrant further examination. Overall, a strong relationship between body size and foraging behavior is to be expected, especially in ruminants. Smaller ruminants typically browse on woody plants such as tree seedlings and saplings (Laskurain et al., 2013; Abraham et al., 2018), while larger ones like bovines are mainly grazers. This distinction in foraging strategies suggests a correlation between livestock size and their impact on agroforestry regeneration (Hofmann, 1989). Moreover, the foraging behaviors associated with livestock size can distinctly affect various life stages. Namely, small ruminants, particularly sheep and goats, might significantly predate acorns akin to wild ungulates (Leal et al., 2022). Further, goats, known for consuming acorns and browsing oak seedlings and saplings (Papachristou et al., 2005; Froutan et al., 2015), are expected to be more harmful than predominantly grazing cattle (Papachristou and Platis, 2011). Considering the nuanced effects of livestock size on tree regeneration, the advice by some authors to prefer smaller livestock such as sheep over larger ones like cattle (e.g., López-Sánchez et al., 2016) may not fully consider the potential impacts on acorns, for example. A comprehensive analysis of effect magnitudes across varied studies and conditions is essential to clarify whether livestock 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 the last 33 years. This research synthesis compared grazed versus ungrazed areas in *Quercus*-dominated agroforestry systems to discern the influence of livestock and their size-related foraging behaviors on each of the early life stages of oak trees. We addressed the following questions and hypotheses: (1) Is the combined effect of livestock negative, considering survival of acorns and the survival, growth, and density of seedlings and saplings? Adding to multiple regeneration threats, we hypothesize that livestock would have an overall negative effect. (2) Do livestock effects vary in sign and magnitude among acorn, seedling, and sapling stages? Given some oak seedlings and saplings' resilience to above-ground tissue mortality—a trait not shared by acorns—we hypothesize distinct effects by stage. (3) Does the effect on oak early stages vary with livestock size and associated foraging behaviors? Given this association, we expect significant variations in effects based on livestock size. Owing to goats' known impact across early life stages, we anticipate more negative outcomes in studies involving goats and less marked with mixed-size livestock. (4) Does the effect on oak life stages differ by the metric used in studies? Given young oaks' resilience to grazing, which can include resprouting, we anticipate less negative effects on survival, but greater variability in growth and density metrics. 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 Science, Biodiversity Conservation, Environmental Science, 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 search string criteria: Allred et al., 2012; Laskurain et al., 2013; and Griswold and Koenig, 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 groups: (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 (cows, horses), small (sheep, goats), or mixed.

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, addressing the issue of pseudo-replication (Massad and Dyer, 2010) across a total of 54 case studies. 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.

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 America (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. 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 cows and sheep (67% of mixed-size studies) or a combination of cows, 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 cows. 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 (τ^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 (τ^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 24 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 9 involving small-sized and 5 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. 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. 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 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 Africa, our findings highlight a consistent negative influence. The overall effect size, quantified using Hedge's *d*, substantiates the significance of this endeavor, with an effect size of -0.87 (95% CI: [-1.12, -0.62]). Our results have implications for global agroforestry system regeneration, particularly given the economic importance of declining *Quercus* species.

4.1. Effects on early oak life stages

Our synthesis reveals that livestock exert a consistently detrimental impact on 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 (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 26 case studies. This included four case studies where livestock had a positive effect. However, most studies indicate higher seedling survival within livestock exclosures over grazed areas, highlighting the detrimental effects of livestock on seedlings through consumption, soil compaction, altered soil properties, and the elimination of microhabitats and dead plant matter, while also likely creating new ecological niches (Etchebarne et al., 2016; Moradi et al., 2021). Despite challenges, the varied effects in case studies underscore resilience and occasional benefits to seedling development from livestock presence, such as enhancing survival by reducing competition from vegetation like annual grasses, while the resilience of oak seedlings to above-ground tissue mortality, with potential for sprouting (Zhang et al. 2019; Vaz et al. 2019), may help mitigate grazing impacts. This resilience is influenced by various factors, including livestock management practices (Pulido et al., 2010), specific oak taxa (Fortuny et al., 2020), and local environmental conditions (Jones, 2000; Plieninger et al., 2004). Some oak species or individual seedlings may show compensatory growth or adaptive responses to grazing, with significant context-dependent variations (Drexhage and Colin, 2003).

Our synthesis uniquely distinguishes livestock impacts on oak seedlings and saplings, unveiling a 'very high' negative impact on saplings (Cohen, 1988). The recovery of all above-ground tissue mortality through sprouting, while likely in younger seedlings, is hindered in saplings by depleted underground acorn reserves and frequent livestock grazing (Roula et al., 2019). 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). 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 size

Our 54 case studies reveal that livestock size, ranging from smaller animals like sheep to larger ones like cows, significantly influences their impact on early oak life stages in agroforestry systems. Small-sized livestock, particularly sheep and occasionally goats—represented by only two case studies exclusively on goats—show more detrimental effects on oak development from acorns to saplings than large-sized or mixed-size groups. This trend is stark in acorn survival, where smaller ruminants seem to be more acorn-predatory than cattle. Sheep compromise seedlings through browsing and trampling, leading to bare soil by removing 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 mixed-size livestock in oak agroforestry systems reduce negative impacts on early oak stages more than systems with only small 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). Maintaining a variety of animal sizes also offers greater economic flexibility to farms (Anderson et al., 2012). Our synthesis further underscores the role of mixed-size livestock in promoting oak agroforest regeneration.

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 cows and sheep. Although both are grazers, their distinct foraging behaviors, stemming from eco-physiological adaptations, can create greater vegetation heterogeneity (Hodgson et al., 1991; Benavides et al., 2009), potentially influencing oak establishment less than in areas with only sheep. While cows, 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). This selectivity allows them to graze on the delicate leaves of oak seedlings and saplings. The remaining case studies within this mixed-size subgroup were split between combinations of cows, 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 cows, 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 cows 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

Despite livestock's generally negative impact, our meta-analysis indicates that mixed-size livestock systems are less harmful for oak regeneration, especially compared to small-sized livestock 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. Our synthesis highlights the significant negative effect of small livestock, particularly sheep and goats, on acorn survival. To enhance oak regeneration, individual protection of saplings and creating fenced areas (Vaz et al., 2019; Löf et al., 2021) to exclude livestock during acorn seasons are crucial for reducing acorn over-predation and promoting survival and early growth. 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 cows, 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 meta-analysis, which suggests benefits of mixed-size livestock grazing. 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, considering how livestock size and climatic conditions, including drought, interact is important 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).

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 cows 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 cows, horses, and sheep. Furthermore, all studies addressing the effects of larger livestock have exclusively examined cows. 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 consistent, high negative effect on early oak life stages linked to livestock size-related 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. Effective oak regeneration strategies should incorporate diverse livestock sizes and consider measures like sapling protection and livestock-excluded areas during acorn seasons. 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.

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Table 1. Summary of articles. Livestock: S = sheep; G = goat; C = cow; 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*
RuizMirazo & 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

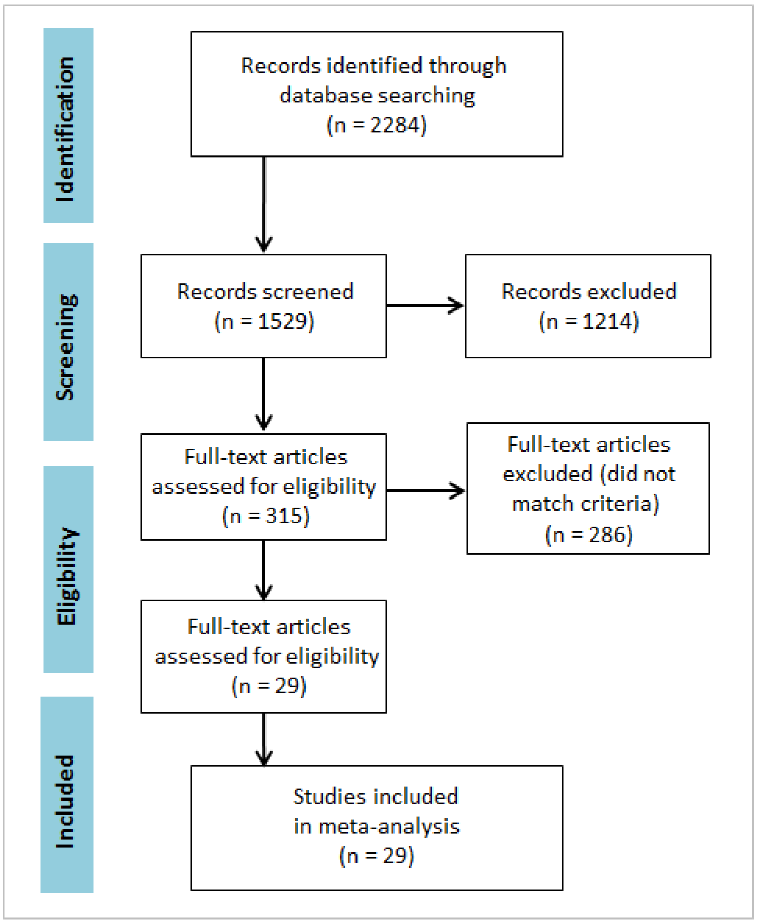

Fig. 1. PRISMA diagram illustrating the study selection process.

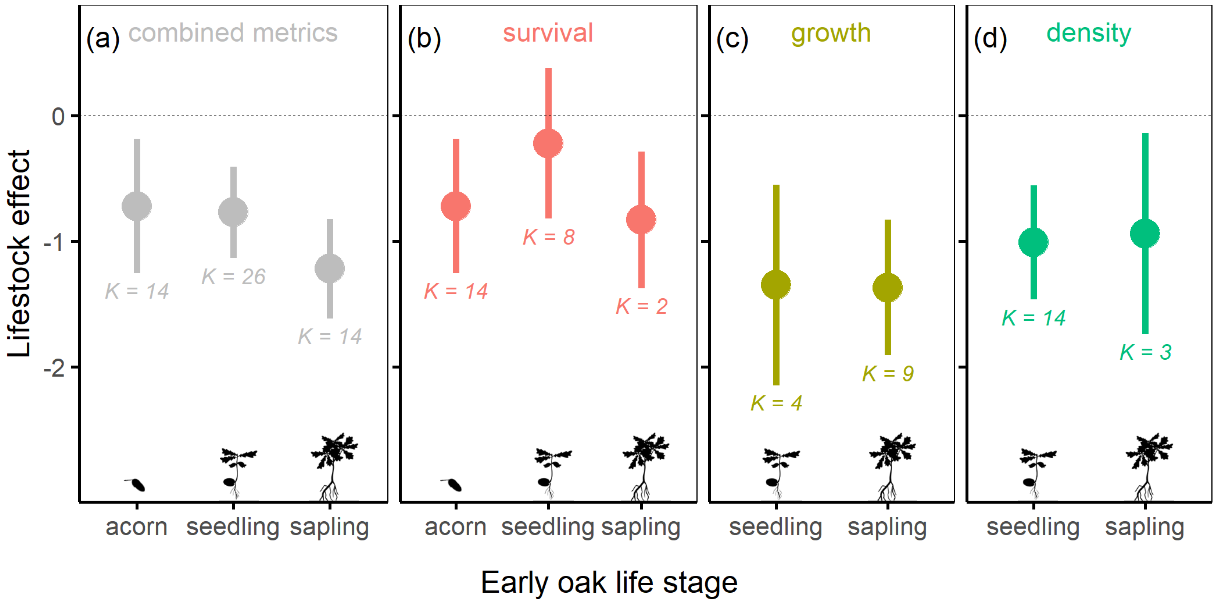

Fig. 2. Mean effect size (Hedges' *d*) of domestic livestock on combined survival, growth, and density effects across life stages (a), and on survival, growth, and density individually (b, c, d). Dots with error bars represent model parameter estimates and their 95% confidence intervals (CI). '*K*' denotes 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).

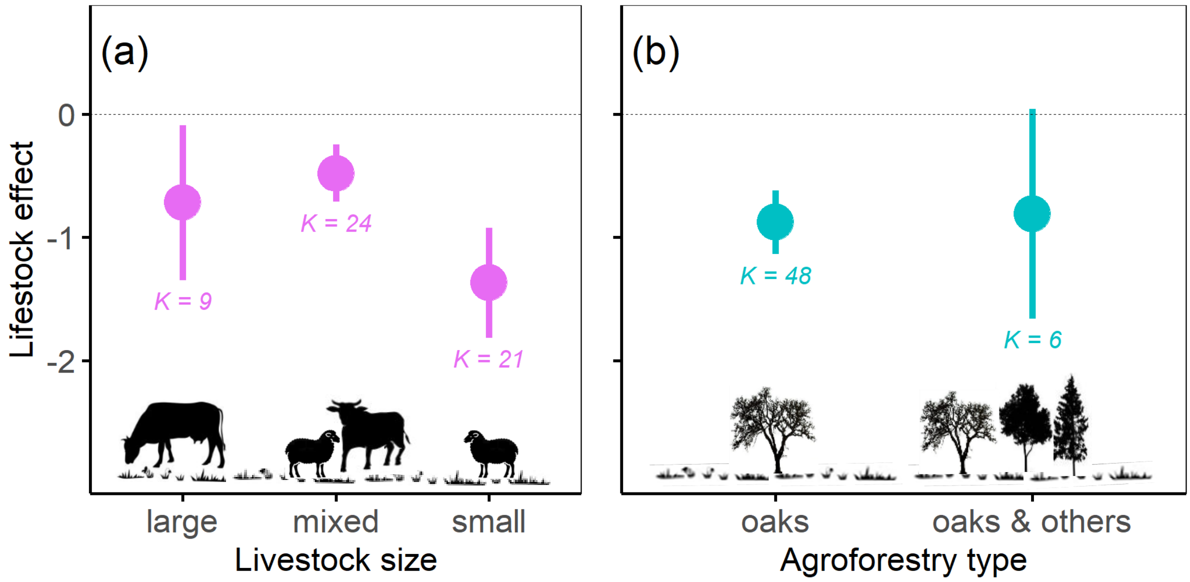

Fig. 3. Mean effect size of domestic livestock on the early life stages of oaks, categorized by body size (a) and type of agroforestry system (b; either oak trees only or oaks mixed with broadleaves and/or conifers). Refer to Figure 2 for more explanations.