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EDITED BY

John D. C. Linnell,
Norwegian Institute for Nature Research
(NINA), Norway

REVIEWED BY

Annika Zuleger,
Martin Luther University of Halle-
Wittenberg, Germany
Anchal Bhasin,
National Tiger Conservation Authority
(NTCA), India

*CORRESPONDENCE

Lucia Cattani
✉ cattani.lucia@spes.uniud.it

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Agro-livestock practices and wild ungulates in shared landscapes: a systematic review on trophic competition, spatio-temporal interactions, and agricultural damage

Lucia Cattani*, Mirco Corazzin, Stefano Bovolenta,
Edi Piasentier and Marcello Franchini

Department of Agricultural, Food, Environmental and Animal Sciences, University of Udine, Udine, Italy

Introduction: Over the past few decades, European agricultural landscapes have undergone contrasting processes of intensification in lowland areas and abandonment of marginal territories. This spatial polarization, in conjunction with the expansion of wildlife populations, has increased interactions and potential conflicts in shared landscapes. This systematic review aims to synthesize the current evidence on the interactions between wild ungulates and agro-livestock systems (excluding forest and shrubland habitats) in Europe, specifically focusing on trophic competition, spatio-temporal dynamics, and agricultural damage, while identifying the main trends and research gaps.

Methods: Following PRISMA guidelines, a systematic search was conducted on the Scopus database in January 2026, covering literature published up to December 2025. Studies were included if they investigated interactions between wild and domestic ungulates or their outcomes in terms of agricultural damage. Studies focusing on predation, damage to forestry or orchards, stakeholder perceptions, and disease transmission were excluded.

Results: After the screening process, 58 studies published between 1984 and 2025 were included. Findings revealed that a large number of studies were conducted in Italy, accounting for 17 out of 58 studies (29.31%). Additionally, wild boar (29 out of 58 studies - 50.00%) and red deer (24 out of 58 studies - 41.38%) were the most represented species. The review identified 19 out of 58 studies (32.76%) on trophic competition, 16 studies (27.59%) on spatio-temporal interactions, and 38 (65.52%) on agricultural damage. The results indicate that wild boars are primarily responsible for agricultural damage. Moreover, trophic competition most frequently occurred through reductions in forage availability caused by high wild ungulate densities. Conversely, findings on spatio-temporal dynamics suggest reciprocal pressure, highlighting that livestock often displace wild ungulates from optimal foraging sites, mainly due to high densities or indirect human-related disturbances.

Discussion: These findings suggest that enhancing human-wildlife coexistence requires an integrated management approach, combining population controls with non-lethal preventive measures. Furthermore, standardized monitoring and farmer involvement in research are necessary to develop effective mitigation strategies.

KEYWORDS

agro-ecosystems, crop raiding, human-wildlife conflict, land abandonment, passive rewilding, PRISMA method, resource partitioning, wildlife management

1 Introduction

European agricultural landscapes are currently defined by a pronounced spatial polarization, a trend that has accelerated over the last few decades (MacDonald et al., 2000; Dax et al., 2021). Agricultural production and livestock farming activities have increased significantly in the most fertile and accessible lowland areas, where technological advancements and support from the Common Agricultural Policy (CAP) have maximized efficiency and productivity (Quintas-Soriano et al., 2022). Simultaneously, marginal territories, particularly hilly and mountainous regions, have faced progressive abandonment due to high production costs, heavy labor requirements, and low economic profitability (Battaglini et al., 2014; Ustaoglu and Collier, 2018; Dax et al., 2021). In this context, the agricultural and livestock farming crisis is further exacerbated by an aging workforce and a significant lack of attractiveness for younger generations, who often perceive insufficient social recognition for the farming profession (Coopmans et al., 2021; Borda et al., 2023).

Conversely, the extensive, grass-based livestock systems still operating in these areas are considered multifunctional (Rodríguez-Ortega et al., 2014; Pachoud et al., 2020) because, in addition to their potential to produce high-quality food, they provide important ecosystem services (Millennium Ecosystem Assessment, 2005; TEEB, 2010; Haines-Young and Potschin, 2012). These services encompass landscape maintenance, mitigation of natural hazards such as wildfires and soil erosion, and biodiversity conservation (Battaglini et al., 2014; Pachoud et al., 2020). However, the impact of such systems on biodiversity is complex and involves trade-offs. While livestock grazing may exert competitive pressure on limited resources or cause the spatial displacement of wildlife (Acevedo et al., 2007; Feng et al., 2021), its complete removal does not necessarily prevent negative consequences (Chaikina and Ruckstuhl, 2006).

The progressive abandonment of these practices has driven processes of “passive rewilding” (Pereira and Navarro, 2015). While excluding livestock may increase the abundance of certain species (Filazzola et al., 2020), uncontrolled vegetation regeneration due to the cessation of management practices can lead to habitat closure through bush encroachment, loss of landscape mosaics, and increased risk of wildfires, ultimately threatening cultural landscapes and open-habitat biodiversity (Chaikina and Ruckstuhl, 2006; Pereira and Navarro, 2015; Bugalho et al., 2026). In this scenario, ‘agricultural rewilding’ models have been proposed as an integrated approach, conceptually situated between agroecology and pure rewilding (Gordon et al., 2021; Corson et al., 2022; van Dooren et al., 2025). Consequently, the remaining extensive farms now face the necessity to manage increasingly complex interactions with recovering wildlife populations (Carpio et al., 2021; Franchini et al., 2021, 2025).

Indeed, in parallel with the retreat of human-managed activities, Europe has transitioned into an era of widespread “wildlife return” (Ledger et al., 2022). After decades of decline mainly attributable to habitat loss and human persecution, wild populations have progressively started to recolonize their former historical ranges (Burbaité and Csányi, 2010; Valente et al., 2020; Ionescu et al., 2025). Recent estimates have shown that approximately 90%

of the European continent is now inhabited by at least one native wild ungulate species (Linnell et al., 2020). This resurgence is driven by a combination of more restrictive hunting legislation, active reintroduction programs, conservation initiatives, and large-scale socio-economic changes (Linnell et al., 2020; Ledger et al., 2022). Land abandonment has led to expanding wild habitats and increased forage availability, transforming rural areas into shared landscapes where domestic and wild species increasingly overlap (Linnell et al., 2020). While human-wildlife conflict research mostly focuses on livestock predation by carnivores (e.g., Ridwan et al., 2023; Abas et al., 2025; Franchini et al., 2025, 2026), co-occurrence between wild and domestic ungulates can also represent a source of conflict (e.g., Martin et al., 2011; Chirichella et al., 2014; Valente et al., 2020; Jiménez-Ruiz et al., 2022). Human-wildlife conflicts should therefore be considered a multifaceted problem, encompassing various aspects related to the interactions between human activities and wild species in shared landscapes (Nyhus, 2016). These interactions extend beyond the transmission of shared infectious diseases, such as bovine tuberculosis and African swine fever, and manifest through intense trophic competition, spatio-temporal dynamics, and agricultural damage (e.g., Bobek et al., 2017; Franchetto et al., 2025; Unsgård et al., 2025).

In managed agro-livestock systems (here defined as excluding forest and shrubland habitats), ecological interactions involving wildlife and livestock frequently translate into socio-economic impacts on farmers, making the distinction between purely ecological processes and human-wildlife conflicts less evident (Chirichella et al., 2014; Schieltz and Rubenstein, 2016). Indeed, when wildlife impacts occur on pastures, meadows, or crops intended for livestock feed (e.g., maize and field cereals), economic losses may result from reduced forage availability for livestock (Bueno et al., 2010; Corgatelli et al., 2019). In this sense, the process of trophic competition may occur through interference, i.e., direct social interactions and/or exploitation of food resources (Chirichella et al., 2014). Studies have shown that these effects are often asymmetrical. Domestic livestock, usually superior in density and body size, often displace wild species to suboptimal habitats (Brivio et al., 2022). Conversely, high densities of wild ungulates can significantly reduce the availability of high-quality forage for cattle (*Bos taurus*) and sheep (*Ovis aries*), particularly during seasonal bottlenecks (Unsgård et al., 2025).

However, interactions between wild and domestic herbivores are not exclusively competitive. They can also manifest as facilitation, where the grazing activity of one species improves resource quality for another (Kuiters et al., 2005; Chirichella et al., 2014). For instance, cattle grazing can stimulate grass regrowth, enhancing its nutritional value for red deer (*Cervus elaphus*) (Kuiters et al., 2005). Nonetheless, when resources, such as sward height, fall below critical thresholds, competition typically prevails (Gordon and Illius, 1989; Kuiters et al., 2005). Resource partitioning is therefore highly dynamic and seasonally dependent, with dietary overlap peaking when food is abundant but becoming a source of conflict when food availability is limited.

Behaviorally, species adjust their spatio-temporal activity in response to the presence or absence of other species, resulting in complex spatio-temporal dynamics (Barasona et al., 2014; Chirichella et al., 2014;

Franchetto et al., 2025). Spatial segregation and avoidance are common strategies adopted by wild ungulates to reduce competition in high livestock density areas (Chaikina and Ruckstuhl, 2006; Chirichella et al., 2013; Forti et al., 2021). Furthermore, spatial avoidance is adopted to better counteract the effects of human activities, livestock management routines (e.g., milking), or the presence of livestock guardian dogs (LGDs) (Mattiello et al., 2003; Chirichella et al., 2013; Weiss et al., 2022).

Recent technological advances, such as GPS telemetry and camera-trapping, have revealed that wild-domestic ungulate interactions rarely involve physical aggressions, but are often driven by indirect mechanisms (Franchetto et al., 2025). Wild ungulates may shift their habitat selection to avoid pastures intensively used by livestock (Mattiello et al., 2002), returning only when cattle or humans are absent (Kuiters et al., 2005). Wild ungulates may also avoid specific areas due to the presence of livestock and the associated olfactory cues (Frid and Dill, 2002; Chirichella et al., 2013; Weiss et al., 2022). Furthermore, management practices like supplementary feeding can create artificial aggregations, increasing interaction rates and potentially exacerbating both competition and disease transmission risks (Putman and Staines, 2004; Gortázar and Fernández-de-Simon, 2022).

The rising densities of wild ungulates have significantly increased damage to the agricultural sector, affecting both mountain and lowland farming systems (e.g., Linnell et al., 2020; Valente et al., 2020; Cecchini et al., 2024). Moreover, when damage involves crops or grasslands intended for animal feed, the economic loss is associated with indirect trophic competition resulting from reduced forage availability for livestock. Wild boar (*Sus scrofa*), through rooting and crop consumption, represents the main wild species responsible for up to 95% of agricultural damage across Europe (Valente et al., 2020).

However, red deer can also cause substantial damage, primarily through biomass consumption in forage crops and permanent meadows (Marchiori et al., 2012; Unsgård et al., 2025). Heavy grazing exerted by red deer is indeed not only associated with a quantitative reduction in grass resources, but also with a reduction in the crude protein content of residual forage, in turn increasing supplementation costs for farmers (Marchiori et al., 2012). These damages are linked to the spatial landscape configuration, with a higher risk of damage observed in those fields near forest edges, and/or in areas characterized by high ungulate densities (Amici et al., 2012; Hjermann et al., 2025).

Although human-wildlife conflicts have been extensively investigated, especially in recent years (Torres et al., 2018), most of the existing literature remains fragmented and often restricted to single species or localized study areas. To date, to the best of our knowledge, an integrated, systematic synthesis conducted at the European level examining the triad involving trophic competition between wild and domestic ungulates, spatio-temporal interactions, and agricultural damage within a single conceptual framework is currently lacking. Understanding these dynamics is essential to develop context-specific management strategies that promote co-existence, while ensuring the sustainability of multifunctional farming systems. The primary objective of this systematic review is therefore to synthesize current evidence across Europe, focusing on open and managed agro-livestock systems (thus excluding forest

and shrubland habitats), identifying key trends, research gaps, and conflict-prone areas.

2 Material and methods

2.1 Literature search

This systematic review was conducted in accordance with the PRISMA guidelines (Page et al., 2021). The literature search was carried out on Scopus in January 2026, following an iterative process of query refinement to identify articles relevant to the topic (i.e., trophic competition and spatio-temporal interactions between wild and domestic ungulates, as well as agricultural damage). Only scientific manuscripts published in English and in peer-reviewed journals up to December 31, 2025, were considered. The following final query string was used: (*loss OR competition OR effect* OR damage* OR conflict* OR forag* OR feed* OR diet* OR spatio* OR spatial OR temporal OR spatio-temporal OR spatial-temporal OR behav* OR interaction* OR dynamic* OR "habitat use" OR "habitat selection" OR occupancy*) AND (*wildlife OR "wild ungulate*" OR "wild boar" OR "Sus scrofa" OR deer* OR "Cervus elaphus" OR "Dama dama" OR "Capreolus capreolus" OR mouflon OR "Ovis musimon" OR chamois OR "Rupicapra rupicapra" OR "Rupicapra pyrenaica" OR "Capra ibex" OR "Capra pyrenaica" OR "Alpine ibex" OR "Iberian ibex" OR ibex OR "wild goat*"*) AND (*agricultur* OR forage OR livestock OR farm* OR husbandry OR "domestic ungulate*" OR cattle OR "Bos taurus" OR sheep OR goat* OR "Ovis aries" OR "Capra hircus"*) AND (*crop OR pasture* OR graz* OR meadow* OR grass**). The query was structured by combining four main concept groups (interaction/competition terms, wild ungulate terms, domestic ungulate/agriculture terms, and specific agro-livestock environment terms) using the Boolean operator AND. To maximize relevance, the search was limited to the "Titles, Abstracts and Keywords" fields (using the Scopus field tag TITLE-ABS-KEY). Only studies conducted in European and non-European Union countries (e.g., United Kingdom) were included. Accordingly, a comprehensive string listing all European countries and their associated demonyms (e.g., Germany OR German, Spain OR Spanish) was incorporated into the final query. This approach was chosen, instead of the standard Scopus geographic filter, to reduce the likelihood of exclusion of relevant European studies authored by researchers affiliated with non-European universities or institutions.

2.1.1 Inclusion and exclusion criteria

The focus of the review was to address the exposure to, or presence of, agro-livestock practices in shared landscapes, as these areas are prone to wild-domestic ungulate interactions. Therefore, to be included in the review, studies had to report on one or more of the following outcomes: (i) spatio-temporal interactions between wild and domestic ungulates; (ii) trophic competition (e.g., diet overlap, resource reduction) between wild and domestic ungulates; or (iii) agricultural damage (e.g., crop or pasture damage). For the

purposes of this review, trophic competition was defined as the process leading to a reduction in forage availability for livestock, encompassing both direct dietary overlap between wild and domestic ungulates and wildlife impacts on forage crops, meadows, or pastures used for animal feed. In this sense, while agricultural damage also involves silvicultural lands (i.e., cultivated forests and shrublands), studies focusing on these habitats were excluded from the research. This definition was adopted to reflect the agro-livestock perspective of the review and does not necessarily correspond to a strict ecological definition of interspecific competition.

2.1.2 Selection process

Since only the Scopus database was used, cross-database deduplication was not required. The selection process started with a first screening based on article titles, and manuscripts were excluded if the title was outside the scope of the review. A second screening phase evaluated abstracts. At this stage, articles were excluded if the topic explored other aspects of the human-wildlife dimension (e.g., livestock predation events, damage to silvicultural lands, stakeholders' attitudes and perceptions toward wildlife, disease transmissions), or if they were either focused on habitat use/selection by wild ungulates without a direct connection to interactions with domestic ungulates or agricultural damage, or on technical accuracy of damage evaluation systems. Three independent reviewers (LC, SB, and MF) conducted the two-step screening process: (i) title screening, to remove out-of-scope records; and (ii) abstract screening, to assess eligibility based on predefined criteria. Any discrepancies were resolved through discussion. Records remaining after these two screening phases were considered potentially relevant and were retrieved for full-text assessment. Documents not available online were obtained by contacting the corresponding authors directly or through the institutional library service. All records meeting the inclusion criteria after full-text evaluation were deemed eligible and retained for the final systematic review.

2.1.3 Data extraction and synthesis

Data extracted from all eligible studies were stored into an Excel database, which included key characteristics such as:

- Study identification (authors, title, publication year, journal).
- Study area.
- Target wild and domestic ungulates species.
- Type of interaction (trophic competition, spatio-temporal interaction, agricultural damage).
- Spatio-temporal parameters (i.e., habitat use and daily/seasonal activity patterns).
- Type of crop damaged.
- General notes.

The eligible studies were then synthesized and categorized into three specific tables divided by topic: trophic competition (Table 1), spatio-temporal interactions (Table 2), and agricultural damage (Table 3). Only wild and domestic species pertinent to the review's aim (i.e., those included in the search query) were reported. References

to other species (e.g., equids, small mammals, predators), occasionally mentioned in the source manuscripts, were excluded. In the 'Results section' (see 3 Results), when specific details were not directly deducible from the tables, the total number of supporting studies was provided and, when numerous studies addressed a specific topic, only the two most recent articles were cited as representative examples.

In the 'Trophic competition' section (see 3.1 *Trophic competition*), where not explicitly specified by the authors, "pastures" and "meadows" were identified based on whether the study area was managed for direct grazing or hay production, respectively. Within this section, studies concerning crop damage were included exclusively when a direct link to livestock production or forage consumption was established by the authors (e.g., silage maize or fodder crops). Conversely, impacts on crops not intended for domestic animal feed were assigned solely to the 'Agricultural damage' section (see 3.3 *Agricultural damage*). Studies explicitly investigating damage to fodder crops were included in both sections (i.e., trophic competition and agricultural damage), as they represent both a trophic overlap and an economic loss for the farming system. Where the domestic species was not explicitly stated, it was inferred from the farm type, when available.

Regarding the 'Agricultural damage' section, to maintain a focus on agro-livestock systems, the analysis encompassed all studies reporting wildlife impacts (e.g., crop consumption, economic losses, or trampled areas) on pastures, meadows, or crop fields potentially intended for livestock forage production (such as maize, sorghum, or autumn-winter cereals), even when an explicit link to livestock farming was not specified in the original text. Given that the final utilization of these crops was not always reported in the original studies, their association with livestock feeding systems should be interpreted as potential rather than definitive. Crop categories were classified as follows:

- Grasslands and forage: pastures, meadows, and crops dedicated to hay or silage production.
- Cereals and grains: annual cereal crops (e.g., oats, wheat, barley) excluding maize.
- Maize: analyzed independently as frequently mentioned in literature.
- Annual and field crops: diverse productions (e.g., legumes and root crops) potentially used for animal feed.
- General or others: broader categories or vague descriptions (e.g., "croplands" or unspecified crops).

3 Results

Overall, 1,233 records were identified through the initial search. Following title screening (first screening), 880 records were excluded, and 353 studies remained. The abstract screening led to the exclusion of 282 articles and to the selection of 71 potentially relevant studies retrieved for full-text evaluation. Six of the 71 papers were not available online and were retrieved by directly contacting the corresponding author or through the university document delivery service.

At the end of the full-text screening, 58 studies were deemed eligible and retained for the review. The complete flow of

TABLE 1 Research referring to trophic competition between wild and domestic ungulates.

Wild species	Domestic species	Type of crop/habitat	Protected area	Reference/s
Red deer	Cattle	Maize	YES	Corgatelli et al. (2019)
		Meadow	NA	Trdan and Vidrih (2008); Trdan et al. (2024); Unsgård et al. (2025)
			YES	Marchiori et al. (2012); Corgatelli et al. (2019)
		Pasture	YES	Mas-Carrió et al. (2025)
			NO	Wilson et al. (2009)
			NA	Gordon and Illius (1989); Trdan et al. (2024)
	Sheep	Meadow	NA	Unsgård et al. (2025)
		Pasture	NO	Wilson et al. (2009)
			NA	Cuartas et al. (2000)
	Goat	Pasture	NA	Gordon and Illius (1989)
Wild boar	Cattle	Pasture	YES	Bueno et al. (2010); Engeman et al. (2016)
			NA	Nasiadka et al. (2025)
	Sheep	Pasture	YES	Bueno et al. (2010); Engeman et al. (2016)
	NA	Meadow	NA	Lombardini et al. (2017); Rutten et al. (2018)
Fallow deer	NA	Meadow	NO	Wilson et al. (2009)
		Cereals	NO	Wilson et al. (2009)
Roe deer	Cattle	Cultivated forbs	YES	Minder (2012)
Chamois	Sheep	Pasture	YES	Espunyes et al. (2019)
Iberian ibex	Goat	Pasture	YES	Moço et al. (2014)

NA, not available information.

information highlighting the distinct phases of the systematic review is summarized in [Figure 1](#).

The 58 included studies were assigned to the different categories, i.e., trophic competition, spatio-temporal interaction, and agricultural damage. Studies addressing more than one topic were assigned to multiple categories.

The publication period ranged from 1984 to 2025. An increasing number of publications was observed across year intervals ([Figure 2](#)). Regarding the research focus, 19 out of 58 studies (32.76%) addressed “trophic competition”, 16 out of 58 (27.59%) focused on “spatio-temporal interactions”, and 38 out of 58 (65.52%) investigated “agricultural damage”.

Geographically, Italy was the country where most studies were performed, i.e., 17 out of 58 studies (29.31%). Additionally, Italy was the most represented country across all topics ([Figure 3](#)). Specifically, with respect to trophic competition, Italy was represented in 4 out of 19 studies (21.05%), followed by United Kingdom and Slovenia, i.e., 3 out of 19 studies (15.79%) each. Italy also accounted for almost half of the research on spatio-temporal interactions, with 6 out of 16 studies (37.50%), and led the agricultural damage category with 11 out of 38 studies (28.95%). A detailed summary of the number of studies carried out across all European countries is provided in [Supplementary Table 1](#).

The most frequently studied wild ungulate species were wild boar, with 29 out of 58 studies (50.00%), and red deer, with 24 out of 58 studies (41.38%). Other species were less represented, i.e., roe deer, 6 out of 58 studies (10.34%), chamois, 5 out of 58 (8.62%), fallow deer, 3 out of 58 (5.17%), mouflon, 2 out of 58 (3.45%), and ibex, 2 out of 58 (3.45%). As far as domestic ungulates are concerned, 21 out of 58 studies (36.21%) focused on cattle and/or their feeding areas (pastures, meadows, crops), while 14 out of 58 studies (24.14%) focused on sheep, and only 7 out of 58 (12.07%) on goats (*Capra hircus*). Considering that our review also included literature analyzing the impacts on crops potentially used for fodder production, nearly half of the studies, i.e., 26 out of 58 (44.83%), did not refer to any domestic species.

The commonly applied methodological approaches and quantitative metrics per category are summarized in [Supplementary Table 2](#).

3.1 Trophic competition

Research on trophic competition, including information on the involved wild and domestic species, the habitat or crop type, as well as the status of the study area (i.e., protected or non-protected), is summarized in [Table 1](#).

TABLE 2 Studies focused on spatio-temporal interactions between wild and domestic ungulates.

Wild species	Domestic species	Type of interaction	Reference/s
Red deer	Cattle	Disturbance	Mattiello et al. (2002)
		Facilitation	Mattiello et al. (2002); Kuiters et al. (2005)
		Spatial overlap/neutral	Mattiello et al. (2003); Gillich et al. (2023)
		Spatial segregation/avoidance	Kuiters et al. (2005); Forti et al. (2021)
		Temporal segregation	Mattiello et al. (2003)
	Sheep	Spatial segregation/avoidance	Osborne (1984); Weiss et al. (2022)
		Temporal segregation	Hester et al. (1999)
	Goat	Spatial segregation/avoidance	Weiss et al. (2022)
Roe deer	Cattle	Spatial segregation/avoidance	Gaudiano et al. (2021)
		Spatial overlap/neutral	Franchetto et al. (2025)
Wild boar	Cattle	Facilitation	Kuiters et al. (2005); Bueno et al. (2010)
		Spatial segregation/avoidance	Kuiters et al. (2005)
		Temporal segregation	Franchetto et al. (2025)
Chamois	Cattle	Spatial segregation/avoidance	Franchetto et al. (2025)
	Goat	Spatial segregation/avoidance	Chirichella et al. (2013)
	Sheep	Spatial segregation/avoidance	Rebollo et al. (1993); Chirichella et al. (2013); Magomedov and Babaev (2023)
Mouflon	Sheep	Spatial segregation/avoidance	Brivio et al. (2022)
	Cattle	Spatial segregation/avoidance	Brivio et al. (2022)
	Goat	Spatial segregation/avoidance	Brivio et al. (2022)
Iberian ibex	Goat	Spatial segregation/avoidance	Acevedo et al. (2007)

Red deer emerged as the most frequently investigated wild species, appearing in 11 out of 19 studies (57.89%), with research focusing on its interaction with cattle or sheep over grassland resources. Regarding domestic species, only two studies have investigated interactions with goats (Gordon and Illius, 1989; Moço et al., 2014). Furthermore, only one study considered livestock as a generic category. In four cases, the studies focused on meadows or pastures specifically used for forage production, without any reference to domestic species (Trdan et al., 2003; Wilson et al., 2009; Lombardini et al., 2017; Rutten et al., 2018).

In most of the reviewed studies, i.e., 16 out of 19 studies (84.21%), trophic competition emerged in the form of reduced livestock forage availability as a consequence of wild ungulate interference. This occurred either through direct biomass removal due to pastures/meadows consumption (e.g., Trdan et al., 2024; Unsgård et al., 2025) or through degradation of fodder production (e.g., Rutten et al., 2018; Nasiadka et al., 2025).

While most studies falling within this category focused on traditional grasslands, three studies addressed different crop types. Red deer was reported to cause more significant losses in maize crops than in permanent meadows (Corgatelli et al., 2019). Conversely, impacts on cereal crops by red and fallow deer were categorized as modest (Wilson et al., 2009), whereas damage caused by roe deer to field crops was reported as negligible, even in areas with high crop availability (Minder, 2012).

Three of the included studies investigated trophic interactions within unconventional settings, ranging from fenced, non-free-ranging environments (Cuartas et al., 2000), to island ecosystems

(Gordon and Illius, 1989), and rewilding areas (Mas-Carrió et al., 2025). Cuartas et al. (2000) reported no significant interspecific trophic competition between sheep and red deer. Gordon and Illius (1989) observed dietary variations between cattle and red deer only in winter, when resources were scarce in both abundance and digestibility. This dynamic contrasts with the majority of the reviewed studies, i.e., 11 out of 19 studies (57.89%) which reported peaks in trophic competition mainly during spring and at the beginning of summer (e.g., Hjermann et al., 2025; Unsgård et al., 2025). Mas-Carrió et al. (2025) found that, despite strong dietary overlap, an increase in red deer density led this species to consume different plant taxa to reduce niche overlap, whereas fluctuations in cattle density did not lead to changes in their respective diets.

Considering the methods used, 7 out of 19 studies (36.84%) employed manipulative field experiments using exclusion cages to compare biomass yield and forage quality (e.g., crude protein) between grazed and ungrazed plots (e.g., Trdan et al., 2024; Unsgård et al., 2025). The analysis of fecal samples was another method used in 5 out of 19 studies (26.32%) to indirectly infer competition through niche overlap (e.g., Espunyes et al., 2019; Mas-Carrió et al., 2025) and provide information on diet composition.

3.2 Spatio-temporal interactions

Research on spatio-temporal interactions, reporting the involved wild and domestic species along with the specific type of interaction, is summarized in Table 2.

TABLE 3 Research on agricultural damages by wild ungulates.

Wild species	Type of crop/habitat	Measurement of damage	Reference/s
Wild boar	Maize	Compensation amount	Schley et al. (2008); Novosel et al. (2012); Bobek et al. (2017, 2025); Cappa et al. (2019, 2021)
		Damaged area	Schley et al. (2008); Giménez-Anaya et al. (2016); Bobek et al. (2017, 2025); Rutten et al. (2018); Cappa et al. (2019); Mauri et al. (2020)
		Economic loss	Bleier et al. (2012); Rutten et al. (2018)
		N° of events/reports	Geisser and Reyer (2004); Schley et al. (2008); Novosel et al. (2012); Giménez-Anaya et al. (2016); Bleier et al. (2017); Cappa et al. (2019, 2021); Mauri et al. (2020); Rutten et al. (2020); Cecchini et al. (2024); Bobek et al. (2025)
	Grasslands and forage	Compensation amount	Schley et al. (2008); Amici et al. (2012); Novosel et al. (2012); Frackowiak et al. (2013); Bobek et al. (2017, 2025); Cappa et al. (2021)
		Damaged area	Schley et al. (2008); Bueno et al. (2010); Frackowiak et al. (2013); Engeman et al. (2016); Giménez-Anaya et al. (2016); Bobek et al. (2017, 2025); Rutten et al. (2018); Mauri et al. (2020); Nasiadka et al. (2025)
		Economic loss	Lombardini et al. (2017); Rutten et al. (2018); Gren et al. (2020)
		N° of events/reports	Geisser and Reyer (2004); Wilson (2004); Schley et al. (2008); Thurfjell et al. (2009); Novosel et al. (2012); Giménez-Anaya et al. (2016); Lombardini et al. (2017); Mauri et al. (2020); Rutten et al. (2020); Cappa et al. (2021); Cecchini et al. (2024); Bobek et al. (2025); Nasiadka et al. (2025)
	Cereals and grains	Compensation amount	Schley et al. (2008); Novosel et al. (2012); Frackowiak et al. (2013); Bobek et al. (2017, 2025); Cappa et al. (2019)
		Damaged area	Schley et al. (2008); Frackowiak et al. (2013); Giménez-Anaya et al. (2016); Bobek et al. (2017, 2025); Cappa et al. (2019); Mauri et al. (2020); Nasiadka et al. (2025)
		Economic loss	Bleier et al. (2012); Lombardini et al. (2017); Gren et al. (2020)
		N° of events/reports	Geisser and Reyer (2004); Schley et al. (2008); Novosel et al. (2012); Ficetola et al. (2014); Giménez-Anaya et al. (2016); Lombardini et al. (2017); Cappa et al. (2019); Mauri et al. (2020); Widén et al. (2022); Bobek et al. (2025); Nasiadka et al. (2025)
	Annual and field crops	Compensation amount	Schley et al. (2008); Amici et al. (2012); Novosel et al. (2012); Frackowiak et al. (2013); Cappa et al. (2019); Bobek et al. (2025)
		Damaged area	Schley et al. (2008); Frackowiak et al. (2013); Cappa et al. (2019); Mauri et al. (2020); Bobek et al. (2025); Nasiadka et al. (2025)
		Economic loss	Bleier et al. (2012); Gren et al. (2020)

(Continued)

TABLE 3 Continued

Wild species	Type of crop/habitat	Measurement of damage	Reference/s
	General or others	N° of events/reports	Schley et al. (2008); Novosel et al. (2012); Ficetola et al. (2014); Cappa et al. (2019); Mauri et al. (2020); Bobek et al. (2025); Nasiadka et al. (2025)
		Compensation amount	Schley et al. (2008); Bobek et al. (2017)
		Damaged area	Schley et al. (2008); Bobek et al. (2017); Mauri et al. (2020)
		Economic loss	Bleier et al. (2012)
		N° of events/reports	Geisser and Reyer (2004); Schley et al. (2008); Rutten et al. (2019); Mauri et al. (2020); Davoli et al. (2022)
Red deer	Maize	Damaged area	Mauri et al. (2020)
		Economic loss	Bleier et al. (2012); Corgatelli et al. (2019)
		N° of events/reports	Mauri et al. (2020)
		Production loss	Corgatelli et al. (2019)
		Other	Kamler and Homolka (2016)
	Grasslands and forage	Damaged area	Mauri et al. (2020)
		Economic loss	Corgatelli et al. (2019); Trdan et al. (2024)
		N° of events/reports	Mauri et al. (2020)
		Production loss	Trdan et al. (2003); Trdan and Vidrih (2008); Wilson et al. (2009); Marchiori et al. (2012); Corgatelli et al. (2019); Unsgård et al. (2025)
		Other	Hjermann et al. (2025)
	Cereals and grains	Damaged area	Mauri et al. (2020)
		Economic loss	Bleier et al. (2012)
		N° of events/reports	Mauri et al. (2020); Widén et al. (2022)
		Other	Kamler and Homolka (2016)
	Annual and field crops	Damaged area	Mauri et al. (2020)
		Economic loss	Bleier et al. (2012)
		N° of events/reports	Mauri et al. (2020)
	General or others	Damaged area	Mauri et al. (2020)
		Economic loss	Bleier et al. (2012)
		N° of events/reports	Mauri et al. (2020)
Roe deer	Maize	Damaged area	Mauri et al. (2020)
		N° of events/reports	Mauri et al. (2020)
		Other	Kamler and Homolka (2016)
	Grasslands and forage	Damaged area	Mauri et al. (2020)
		N° of events/reports	Mauri et al. (2020)
		Other	Minder (2012)
	Cereals and grains	Damaged area	Mauri et al. (2020)
		N° of events/reports	Mauri et al. (2020); Widén et al. (2022)
		Other	Minder (2012); Kamler and Homolka (2016)
	Annual and field crops	Damaged area	Mauri et al. (2020)
		N° of events/reports	Mauri et al. (2020)
		Other	Minder (2012)

(Continued)

TABLE 3 Continued

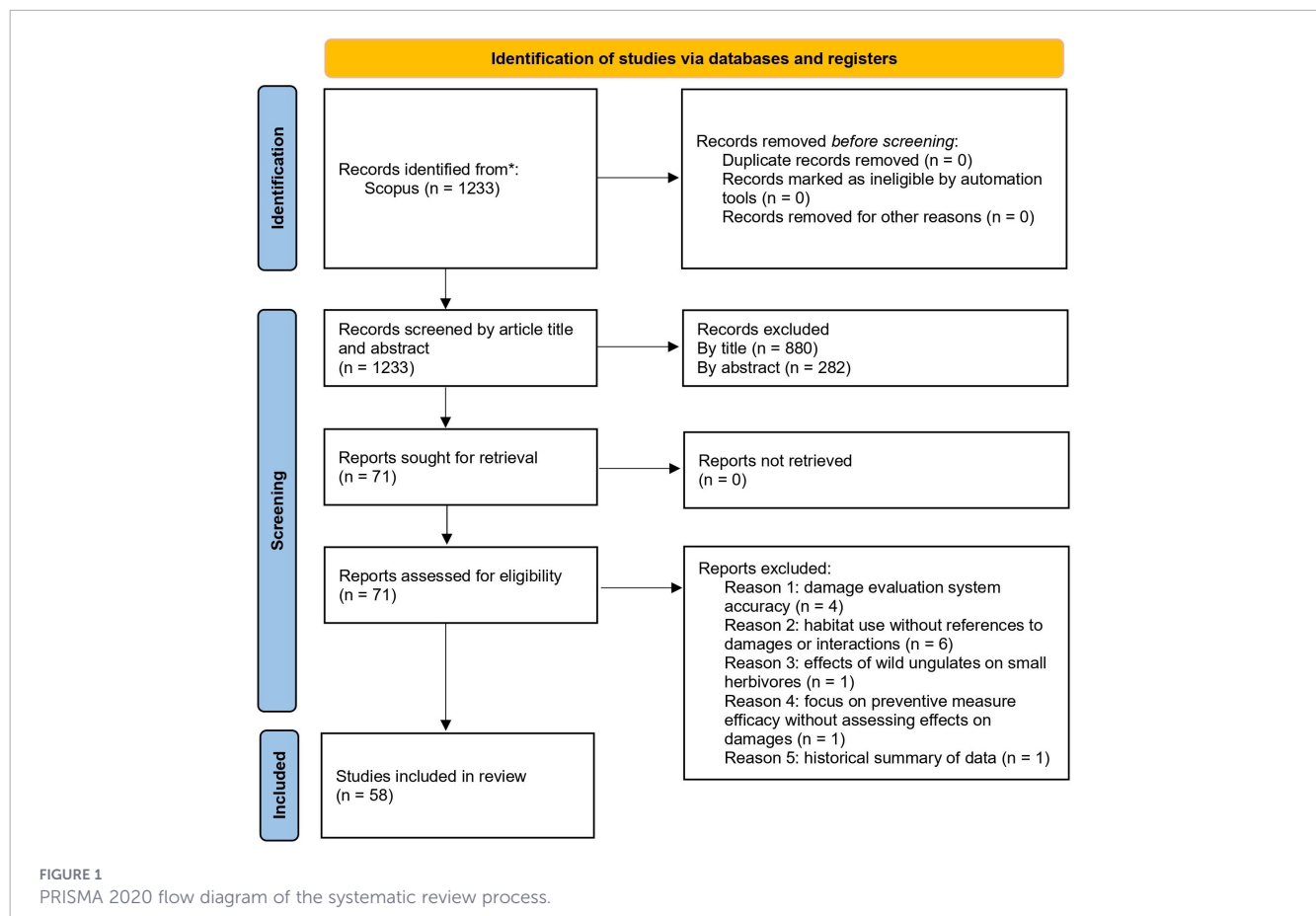
Wild species	Type of crop/habitat	Measurement of damage	Reference/s
Fallow deer	General or others	Damaged area	Mauri et al. (2020)
		N° of events/reports	Mauri et al. (2020)
	Grasslands and forage	Production loss	Wilson et al. (2009)
	Cereals and grains	Economic loss	Menichetti et al. (2019)
		N° of events/reports	Widén et al. (2022)
Mouflon	Maize	Other	Wilson et al. (2009); Menichetti et al. (2019)
	Cereals and grains	Other	Kamler and Homolka (2016)

The red deer emerged as the wild ungulate most frequently investigated in this context, i.e., 10 out of 16 studies (62.50%). Regarding domestic ungulates, cattle and sheep were the most represented, appearing in 10 out of 16 (62.50%) and 7 out of 16 studies (43.75%), respectively.

Spatial segregation and avoidance were the predominant observed behaviors, highlighted in 11 out of 16 studies (68.75%), where domestic species were reported to displace wild ungulates. This displacement was most frequent between red deer and cattle or sheep, i.e., 6 out of 16 studies (37.50%) (e.g., Forti et al., 2021; Weiss et al., 2022), followed by chamois avoiding sheep, i.e., 3 out of 16 studies (18.75%) (e.g., Chirichella et al., 2013; Magomedov and Babaev, 2023). Beyond spatial displacement, Mattiello et al. (2002) documented the interaction in the

form of increased vigilance by red deer, rather than total displacement. Temporal segregation was reported in 3 out of 16 studies (18.75%), where wild species modified their activity patterns to avoid co-occurrence with livestock (Hester et al., 1999; Mattiello et al., 2003; Franchetto et al., 2025). Facilitation or neutral interactions were also documented in 6 out of 16 studies (37.50%). Facilitation involved wild ungulates using pastures previously grazed by livestock (e.g., Kuiters et al., 2005; Bueno et al., 2010), while neutral interactions were characterized by spatial overlap (Mattiello et al., 2003; Gillich et al., 2023) or co-occurrence with moderate temporal overlap (Franchetto et al., 2025).

Methodologically, spatio-temporal interactions identification relied on a combination of traditional and modern tracking techniques. In



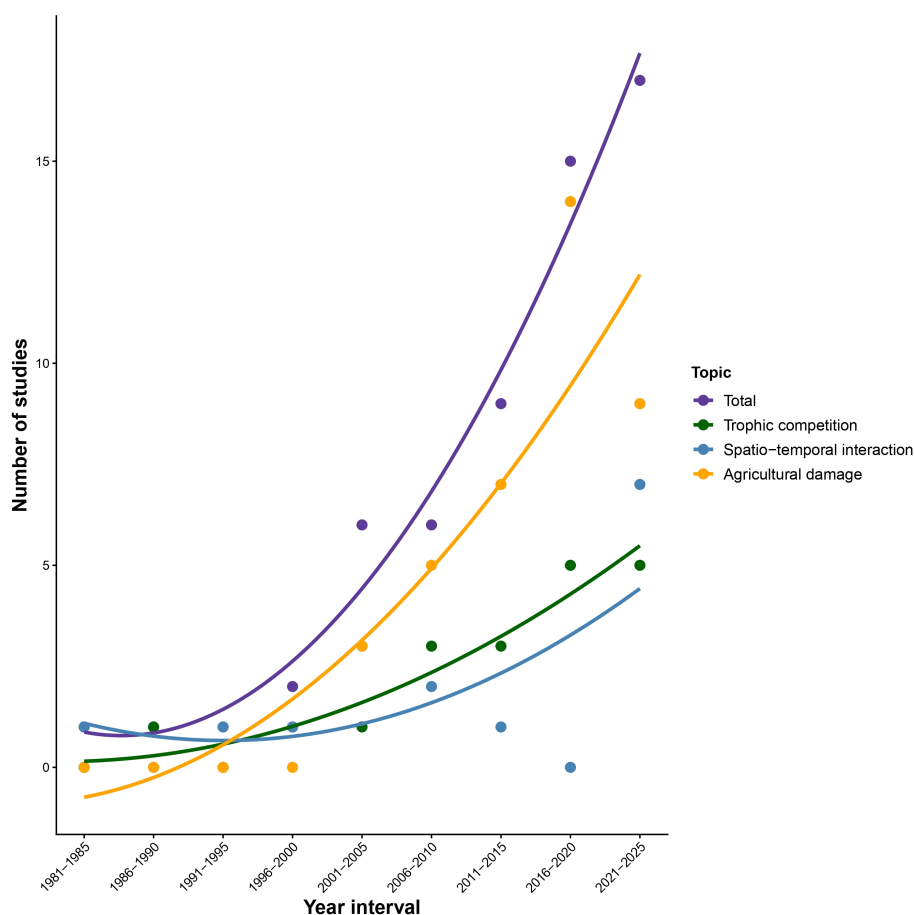


FIGURE 2

Temporal distribution of the reviewed studies (5-year intervals) shown by interaction category and total count. The total count represents unique studies; because some studies were classified into more than one interaction category, the sum of the category counts may exceed the total for a given interval.

some studies, data on activity patterns and habitat use were obtained through GPS telemetry and/or camera-trapping (e.g., Gillich et al., 2023; Franchetto et al., 2025). Indirect indices, such as fecal pellet group counts (e.g., Forti et al., 2021; Gillich et al., 2023), were also used to estimate animal density and spatial distribution.

3.3 Agricultural damage

Research on agricultural damage, reporting the involved wild ungulate species, the affected habitat or crop, and the metric used for damage measurement (e.g., damaged area, production loss), is summarized in Table 3.

Wild boar was reported as the species most frequently involved in agricultural damage, i.e., 29 out of 38 studies (76.32%), followed by red deer, i.e., 13 out of 38 studies (34.21%). Wild boar damage was extensively documented across all crop categories, particularly maize, grasslands, and forage, as well as cereals and grains. Damage was reported in the form of both rooting and direct consumption, leading to reductions in crop production and/or land degradation (e.g., Cappa et al., 2021; Cecchini et al., 2024). Red deer was the second major driver of damage, with research mainly focusing on production losses in grasslands and/or forage crops (Trdan et al., 2024; Unsgård et al., 2025).

Regarding the methodological approach, the literature revealed two primary strategies for data collection. Most studies, i.e., 16 out of 38 (42.11%) (e.g., Bobek et al., 2025; Nasiadka et al., 2025) relied on administrative data such as compensation claims or official reports. Conversely, other studies, i.e., 10 out of 38 studies (26.32%) (e.g., Trdan et al., 2024; Unsgård et al., 2025), used manipulative field experiments including the implementation of exclusion cages to provide a direct measure of yield loss. In some cases, indirect proxies such as fecal pellet counts and rooting area mapping were used to associate the presence of wild animals with the extent of the damage (e.g., Bleier et al., 2012; Engeman et al., 2016).

Nevertheless, the specific metrics used in these studies were highly heterogeneous, in turn complicating direct comparisons of the overall impact. In those studies aimed at quantifying economic losses, compensations were generally estimated based on market prices, but units varied significantly, ranging from euros per damaged hectare or square kilometer (Bleier et al., 2012; Bobek et al., 2025), to euros per lost ton (Amici et al., 2012) or per individual farm (Corgatelli et al., 2019; Gren et al., 2020). Similarly, in studies where the amount of compensation was used to quantify the extent of damage, researchers typically relied on data retrieved from official claims. However, 5 out of 38 studies (13.16%) indicated the mean amount of compensation per case (e.g., Bobek et al., 2017;

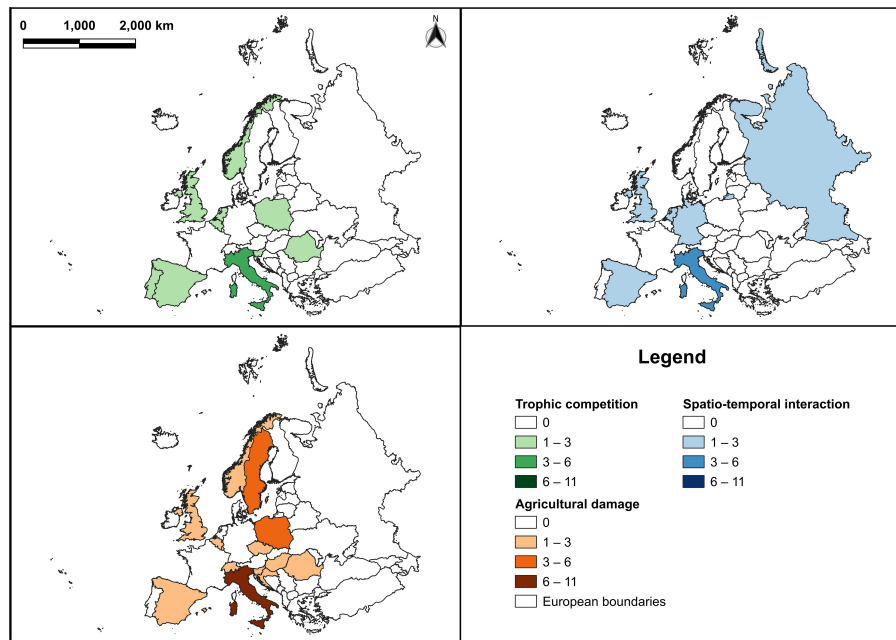


FIGURE 3

Geographic distribution of the selected studies across Europe, categorized by interaction type. The maps illustrate the intensity of research across Europe for (top-left) trophic competition, (top-right) spatio-temporal interactions, and (bottom-left) agricultural damage.

Cappa et al., 2019), while 10 out of 38 studies (26.32%) provided information about the average or total amount of compensation per year (e.g., Corgatelli et al., 2019; Mauri et al., 2020). Furthermore, administrative data often reported the number of damage events (e.g., Cappa et al., 2021; Bobek et al., 2025). Experimental studies reporting production loss typically used either kilograms of dry matter or percentage yield losses relative to potential output (e.g., Marchiori et al., 2012; Unsgård et al., 2025). Research reporting damaged areas mainly referred to the percentage or number of hectares of the affected area, in some cases specifying the type of crop involved; while in other cases providing a general description (e.g., Bobek et al., 2025; Nasiadka et al., 2025).

4 Discussion

The limited number of studies included in this review highlighted the still limited attention on themes including the trophic competition between wild and domestic ungulates, spatio-temporal interactions between wild and domestic ungulates, and agricultural damage in European agro-livestock environments. Our systematic review therefore provides important insights into topics that have received limited attention in the human-wildlife conflict scenario.

Except for the topic referring to agricultural damage, which accounted for a large proportion of studies, research on trophic competition and spatio-temporal interactions is still widely overlooked across Europe. The limited focus on these topics aligns with other systematic reviews on human-wildlife conflicts, where attention has been mostly centered on livestock predation by large carnivores, making interactions with wild ungulates less studied (Su et al., 2022; Ridwan et al., 2023). Furthermore, the scarcity of

studies on these topics may also reflect a mismatch between scientific priorities and herders' perceptions (Pascual-Rico et al., 2020). Although it might appear intuitive to expect that scientific attention focuses on the impacts perceived as most threatening by stakeholders, research on wild ungulates often prioritizes issues with broader societal impacts, such as traffic collisions or human safety, which are frequently addressed in the literature but typically not prioritized by herders. Conversely, impacts that directly affect their livelihoods, such as trophic competition, are generally perceived as more problematic by herders, but remain comparatively understudied.

This paucity of studies may also reflect the scope of the review itself. Indeed, the search strategy was intentionally designed to focus on managed agricultural lands, meadows, and pastures. This choice was made to specifically investigate wild-domestic ungulate interactions within agro-livestock systems. Therefore, the patterns identified in this review should be interpreted within this specific context, rather than as representative of all types of interactions across European landscapes.

The temporal distribution revealed an upward trend in the number of studies focused on wild-domestic ungulates interactions, especially in recent years. This trend is consistent with broader systematic reviews highlighting a general increase in the number of studies on human-wildlife conflicts (Torres et al., 2018; Su et al., 2022; Ridwan et al., 2023; Abas et al., 2025) and may also be related to the widespread recovery of wild ungulate populations across Europe (Valente et al., 2020; Carpio et al., 2021; Ledger et al., 2022; Ionescu et al., 2025). Indeed, factors such as land abandonment in mountainous regions, reforestation, and conservation policies have all contributed to the expansion of wildlife communities (Ledger et al., 2022), ultimately causing an increase in the number of interactions between wild species and agro-livestock farming in

shared landscapes (Chirichella et al., 2014; Valente et al., 2020; Ridwan et al., 2023; Abas et al., 2025). The magnitude of these negative interactions (e.g., competition and damage), especially in conflict-prone areas, fosters negative perceptions of wildlife among stakeholders (Pascual-Rico et al., 2020; Acebes et al., 2024; Miettinen et al., 2026). This has possibly shifted the focus of research toward studies addressing wild-domestic ungulate interactions, as these ecological processes often represent the underlying drivers of broader human-wildlife conflicts. Understanding the mechanisms generating competition, spatial overlap, and agricultural damage is therefore essential for effective conflict management, particularly because perceptions and socio-economic factors strongly influence the magnitude of conflicts (Dickman, 2010).

Although the temporal trend has shown a growing scientific interest in the topic, the geographical distribution of studies revealed disparities across countries. Specifically, a larger proportion of studies was conducted in Italy. This may be attributable to a mix of factors: (i) the increasing abundance of wild ungulate populations, along with their expanded range of distribution in recent decades (Ledger et al., 2022); (ii) high human population densities; and (iii) the presence of a mosaic of agricultural landscapes intermixed with natural vegetation offering shelter and food resources to wild ungulates (Linnell et al., 2020). However, these conditions are not unique across Europe. Alternative explanations may involve differences in research traditions, funding priorities, publication patterns, and the socio-economic relevance of ungulate-related conflicts in specific regions. Moreover, it cannot be excluded that studies from other countries with similar dynamics might be underrepresented, especially if published as grey literature.

The results also showed a species-specific prevalence in the literature, with a primary focus on wild boar and red deer among wild species. This pattern is consistent with other research highlighting the wide distribution of these ungulate species in European agro-ecosystems (Valente et al., 2020; Ledger et al., 2022). The preponderance of studies reporting wild boar damage to agro-livestock activities may be attributed to the species' ecological behavior. Indeed, compared to other ungulate species, the wild boar exhibits notable ecological plasticity and a high reproductive rate, enabling the species to expand rapidly and persist in diverse environmental conditions (Meijaard et al., 2011). Given the frequency and severity of crop damage (Barrios-Garcia and Ballari, 2012), the wild boar is often more negatively perceived compared to other wild ungulates (Pascual-Rico et al., 2020). For instance, Cappa et al. (2021) and Schley et al. (2008) revealed that wild boar is considered the primary agricultural antagonist due to the visible nature of the damage caused. Red deer represent the second most frequently studied species in the reviewed literature, though the nature of the conflict is qualitatively different. In this case, the focus of the research suggested that interactions with red deer are less obvious and primarily localized in meadows and/or pastures, where the species competes with livestock for forage (e.g., Marchiori et al., 2012; Corgatelli et al., 2019). Consequently, the impact is less immediately visible compared to crop damage associated with wild boar presence and behavior. On the other hand, studies on ungulates such as roe deer, chamois, mouflon, and ibex are scarce. The selective browsing behavior of roe deer often results in less

evident damage to forage crops, compared to the mixed feeding and/or rooting behavior of red deer and wild boar, respectively. Regarding chamois and mouflon, they generally occur at lower population densities and are frequently perceived as neutral or beneficial rather than harmful to the environment (Pascual-Rico et al., 2020). Similarly, research on wild goats is largely limited to specific contexts; while Alpine ibex mainly occupy high-elevation alpine areas (Parrini et al., 2009) where domestic livestock are typically absent, Iberian ibex revealed localized dietary overlap when sharing pastures with domestic goats in specific contexts (Moço et al., 2014).

4.1 Trophic competition

As for the trophic competition between wild and domestic ungulates, most of the reviewed studies reported that both wildlife population densities and landscape characteristics are the primary factors influencing these interactions. For instance, high red deer densities may lead to biomass losses in both maize and permanent meadows (Corgatelli et al., 2019; Trdan et al., 2024; Unsgård et al., 2025). This competition can also be intensified by the 'refuge effect' of protected areas in some contexts. In these spots, hunting is restricted or banned, allowing wildlife species to exploit areas in close proximity to meadows and crops (Amici et al., 2012; Marchiori et al., 2012; Corgatelli et al., 2019; Eustace et al., 2022). Moreover, agricultural lands located close to forest edges and/or characterized by high terrain ruggedness are, in certain circumstances, more vulnerable to biomass losses, as terrain ruggedness and forest cover provide refuges for wild species (Lombardini et al., 2017; Hjermann et al., 2025; Unsgård et al., 2025). On the contrary, human infrastructure and urban areas tend to deter wildlife from certain areas (Lombardini et al., 2017; Hjermann et al., 2025). Nevertheless, according to the 'human shield hypothesis', wild ungulates may occasionally move toward more human-dominated areas to seek refuge from predators, which are conversely more sensitive to human disturbance (Berger, 2007; Gaynor et al., 2025).

Moreover, the nature of resource reduction varies depending on the wild species involved. Red deer mainly compete with livestock by directly consuming biomass (Trdan et al., 2024; Unsgård et al., 2025), whereas wild boar cause soil degradation through rooting behavior (Bueno et al., 2010; Barrios-Garcia and Ballari, 2012; Engeman et al., 2016). Bueno et al. (2010) found that wild boar rooting activity affected up to 16% of grazing land, ultimately reducing the surface available for cattle and sheep. Nevertheless, beyond quantitative losses, the effect on forage quality can be complex and sometimes contradictory. Concerning the effects of red deer grazing, studies using exclusion cages showed a reduction in dry matter yield, ranging from a minimum of 11% (Unsgård et al., 2025) to approximately 50% (Trdan et al., 2003, 2024; Trdan and Vidrih, 2008). However, studies on forage quality provided contrasting findings. In some contexts, selective grazing can reduce resource quality through the removal of the most nutritious vegetal components (Marchiori et al., 2012; Corgatelli et al., 2019). Conversely, other studies reported an increase in the quality of grazed plots, as continuous grazing promotes higher crude protein content by maintaining vegetation at an early phenological stage

and stimulating leaf renewal (Trdan et al., 2024; Unsgård et al., 2025). Consequently, depending on the context, interactions initially perceived as trophic competition due to grass consumption by wild ungulates may shift toward trophic facilitation when wild ungulate activity enhances the quality of resources available for domestic species. This finding is consistent with broader ecological studies showing that interactions between livestock and wild herbivores frequently occur along a competition-facilitation continuum rather than representing strictly antagonistic relationships (Chaikina and Ruckstuhl, 2006; Odadi et al., 2011). The balance between these outcomes largely depends on grazing intensity, the density of wild and domestic ungulates, resource availability, and habitat productivity (Schultz and Rubenstein, 2016).

The reviewed studies employed diverse methodological approaches to quantify these impacts. Exclusion cages were primarily used to obtain direct quantitative data on yield loss, enabling a comparison between the quantity and quality of biomass in grazed and ungrazed plots (Corgatelli et al., 2019; Trdan et al., 2024; Unsgård et al., 2025). Additionally, fecal analyses (including microhistological and DNA metabarcoding approaches) provide information on diet composition and, consequently, on niche overlap between the involved species. This may allow researchers to assess species' tendency to shift their food preferences in response to population density and/or resource availability (e.g., Minder, 2012; Espunyes et al., 2019; Mas-Carrió et al., 2025). Finally, drones (UAVs) and photographic estimation represent valuable tools for assessing large-scale forage loss and the associated reduction in forage resources, particularly in highly rugged terrain where the implementation of other methods may be impractical (Engeman et al., 2016; Rutten et al., 2018).

As far as preventive measures and management strategies are concerned, most studies on trophic competition suggested that wild population density controls could represent an effective way to reduce competition (Marchiori et al., 2012; Hjermann et al., 2025; Unsgård et al., 2025), by targeting specific groups rather than using a random approach (Lombardini et al., 2017). Nevertheless, lethal methods are generally less supported by certain stakeholder categories (Zinn et al., 2000; Marchiori et al., 2012; Corgatelli et al., 2019). Fencing could be a more widely accepted measure for protecting crops and may be particularly suitable in conflict-prone areas, such as those near forest edges (Lombardini et al., 2017; Corgatelli et al., 2019; Trdan et al., 2024). However, fence implementation can be expensive, impractical in vast grasslands or croplands, and may negatively impact non-target species (Marchiori et al., 2012; Smith et al., 2020). Other research suggested strategies including growing crops potentially highly attractive to ungulates in areas with high human disturbance (Hjermann et al., 2025). Indeed, high human disturbance often exerts a negative effect on wild ungulate behavior, ultimately reducing damage risk and minimizing resource competition (e.g., Lombardini et al., 2017; Corgatelli et al., 2019; Hjermann et al., 2025).

Although the studies included in the review mainly focused on the effects of wild ungulates on forage resources used by livestock, global evidence suggests that trophic interactions are often reciprocal. High livestock stocking rates, prolonged grazing pressure, and inappropriate pasture management can reduce forage availability

and habitat quality for wild ungulates, whereas moderate grazing regimes may generate facilitative effects by maintaining productive grassland communities (Schultz and Rubenstein, 2016). The predominance of impacts directed from wild species to livestock in this section likely reflects the agro-livestock focus of our search strategy. However, as observed from the 'Spatio-temporal interaction' results (see 3.2 *Spatio-temporal interactions*), this directionality is reversed in spatial dynamics, where livestock exert a dominant displacement effect on wildlife behavior.

4.2 Spatio-temporal interactions

Regarding spatio-temporal interactions between wild and domestic ungulates, the reviewed studies mostly reported the presence of livestock as a significant factor affecting the spatio-temporal behavior of wild ungulates, often leading to wild ungulate displacement from optimal foraging grounds to suboptimal habitats (e.g., Gaudiano et al., 2021; Brivio et al., 2022; Magomedov and Babaev, 2023). Reviewed research on mouflon and chamois has shown that, when livestock are present, these species leave optimal foraging sites in favor of safer but less productive areas, such as rocky terrain or forests (Chirichella et al., 2013; Brivio et al., 2022; Magomedov and Babaev, 2023). A similar spatial displacement toward suboptimal habitats has also been documented for the Iberian ibex in the presence of extensive domestic goat herds (Acevedo et al., 2007). This displacement may lead to higher fitness costs for wild ungulates, as they have to cope with reduced energy intake and/or higher energy costs due to increased movement and vigilance (Frid and Dill, 2002; Mattiello et al., 2002; Mishra et al., 2004). Nevertheless, this displacement usually does not result from direct physical aggression between species. Indeed, Mattiello et al. (2002) found that aggressive interactions are rare, typically involving no physical contact. Conversely, indirect disturbance appeared to be more decisive in causing spatio-temporal segregation. Activities such as livestock husbandry, herder presence, and the use of LGDs are often perceived as threats by wild species (Frid and Dill, 2002; Chirichella et al., 2013; Weiss et al., 2022). For example, milking operations in the field were found to affect the presence of red deer more than the cattle themselves, leading to complete spatial separation during these activities (Mattiello et al., 2003). Furthermore, olfactory cues left by livestock and LGDs can make grazing areas less attractive for weeks after the domestic animals have left (Weiss et al., 2022).

This category provides evidence of reciprocal interactions within the reviewed literature. While trophic competition and agricultural damage were primarily investigated from the perspective of wildlife impacts on agro-livestock systems, studies on spatio-temporal dynamics consistently documented the influence of livestock husbandry practices on wildlife behavior and habitat use. Similar patterns of displacement, avoidance, and behavioral adaptation have been reported worldwide (Schultz and Rubenstein, 2016). These European trends are consistent with global observations at the livestock-wildlife interface. For instance, the spatio-temporal avoidance triggered by livestock presence reflects dynamics in Asian forest landscapes (Feng et al., 2021; Wang et al., 2024). Similarly, in high-altitude environments such as the Himalayas, sheep and goats impose significant resource limitations on native

wild species, often excluding them from optimal pastures (Bagchi et al., 2004; Dahal et al., 2023).

Despite these negative dynamics, shared habitat use by the two categories can sometimes lead to facilitation, which often depends on grazing intensity and timing (Kuiters et al., 2005; Bueno et al., 2010). When grazing intensity is low-to-moderate, it can improve forage quality for wild species by stimulating grass regrowth (Mattiello et al., 2002; Kuiters et al., 2005; Bueno et al., 2010). This may explain why some studies observed red deer and wild boar selecting swards that were previously grazed by cattle (Mattiello et al., 2002; Kuiters et al., 2005). Bueno et al. (2010), for example, found that wild boar in particular showed a preference for areas with moderate stocking rates (between 0.04 and 0.26 LU/ha), likely because livestock grazing reduced vegetation height and altered soil structure, thereby increasing accessibility to below-ground food resources and facilitating rooting activity.

The methods used to explore the spatio-temporal interactions between wild and domestic ungulates influence the resolution at which these interactions are identified and the information obtained. Among the reviewed literature, GPS telemetry and camera-trapping were predominantly used to provide data on habitat use, activity patterns and temporal avoidance behaviors (e.g., Gaudiano et al., 2021; Gillich et al., 2023; Franchetto et al., 2025). Conversely, fecal pellet group counts were employed primarily as an indicator to map wildlife distribution and density over longer periods (Kuiters et al., 2005; Forti et al., 2021). Some authors suggested combining these techniques, since direct observations or camera-traps can provide specific information on individual animal characteristics, while fecal pellet counts provide an overview of wildlife distribution and presence (Mattiello et al., 2003), also enabling researchers to perform fecal analysis and gain information on diet composition (Suter et al., 2004; Fankhauser et al., 2008; Mas-Carrió et al., 2025).

In terms of mitigation and management strategies, some of the reviewed studies on spatio-temporal interactions suggested ways to promote positive coexistence in shared landscapes, while minimizing disturbance to wildlife species and maintaining animal husbandry activities on pastures. A recommendation, particularly for areas where wild ungulates occur at low densities and need protection, is to establish buffer zones around these areas (Brivio et al., 2022). The effectiveness of such zones in reducing disturbance is supported by the identification of specific distance thresholds in certain contexts. Brivio et al. (2022) found that mouflon tend to select optimal feeding sites less frequently when livestock (including free-ranging cattle, goats, and sheep, as well as horses, donkeys, and pigs) roam within 655 meters. Meanwhile, Weiss et al. (2022) found that red deer displacement occurs at distances of up to 3,000 meters from grazing sites used by sheep and goats. Regarding indirect disturbances, Mattiello et al. (2003) suggested that dairy livestock farmers should maintain regular schedules for milking and management to reduce unexpected stimuli, as wild ungulates show adaptation to predictable activities. This recommendation also aligns with other studies supporting the hypothesis that wild ungulates tend to habituate to predictable, non-lethal human activities, despite remaining sensitive to infrequent and unpredictable stimuli (Stankowich, 2008; Brown et al., 2012). Finally, pasture

carrying capacity should be evaluated and livestock overabundance avoided to maintain a balance between wild and domestic ungulate interactions while preventing habitat degradation (Chirichella et al., 2013; Magomedov and Babaev, 2023).

4.3 Agricultural damage

As far as agricultural damage is concerned, the systematic review revealed that, among the three topics considered, agricultural damage has received the greatest attention. This is probably due to the high density and rapid expansion of wild boar, which were identified as the species primarily responsible for damage in the majority of studies (Valente et al., 2020; Cappa et al., 2021; Cecchini et al., 2024).

However, synthesizing these findings into a comprehensive estimate remains challenging due to the notable heterogeneity in the metrics used in the literature. Some studies quantify the impact in economic terms, such as euros per ton, per damaged hectare, or per farm (e.g., Amici et al., 2012; Gren et al., 2020; Bobek et al., 2025), while others use measures derived from manipulative field experiments, such as biomass loss in kilograms of dry matter or percentage of yield reduction (Marchiori et al., 2012; Trdan et al., 2024; Unsgård et al., 2025). The absence of a standardized approach, combined with the site-specific nature of ecological and economic conditions, makes direct comparisons between different geographical regions and crop types challenging.

A limitation that emerged from the reviewed literature lies in the potential underestimation of damage when relying solely on administrative data (e.g., compensation claims). This may occur because farmers may choose not to report damage (especially minor ones) due to bureaucratic complexities, the existence of minimum damage thresholds for eligibility, and/or the limited availability of public reimbursement funds (Ficetola et al., 2014; Cappa et al., 2019; Corgatelli et al., 2019; Mauri et al., 2020). Furthermore, while data on the number of damage events are easily comparable and provide useful frequency trends, they often fail to characterize the actual severity or the qualitative nature of the impact, such as reductions in the crude protein content of residual forage, which can induce additional costs for farmers (Marchiori et al., 2012; Trdan et al., 2024).

Across the reviewed studies, damage was often linked to proximity to forest edges and woodland cover (e.g., Amici et al., 2012; Bleier et al., 2017; Cappa et al., 2019), as well as wild ungulate density (e.g., Hjermann et al., 2025; Unsgård et al., 2025). Indeed, both emerged as factors frequently related to damage occurrence. Crop type and phenology also played a crucial role: maize was found to be most vulnerable during both the sowing and ripening stages (e.g., Lombardini et al., 2017; Cappa et al., 2019), whereas grasslands primarily suffered from biomass consumption by red deer (e.g., Corgatelli et al., 2019; Unsgård et al., 2025) or land degradation caused by wild boar rooting behavior (e.g., Thurfjell et al., 2009; Bueno et al., 2010). Another effect requiring consideration is the so-called “refuge effect”, based on which hunting bans within protected areas or private woodlands create refuges for wild ungulates, thereby increasing the odds of damage in adjacent agricultural fields (Amici et al., 2012; Marchiori et al., 2012).

However, in some contexts, predators can influence this impact. Davoli et al. (2022) showed that the “landscape of fear” created by wolves shifted wild boar damage away from core predator habitats toward more human-disturbed areas. This aligns with the “human shield hypothesis”, suggesting that prey species tend to avoid areas with an elevated predation risk, seeking refuge near anthropic environments, potentially shifting impacts toward more urban and disturbed areas (Berger, 2007; Gaynor et al., 2025).

Finally, the effectiveness of the adopted population control strategies remains under debate. Several studies indicated that current levels of harvesting often fail to significantly reduce the extent of agricultural damage or limit population growth (e.g., Cappa et al., 2021; Cecchini et al., 2024). In some cases, harvesting can even trigger an increase in population size the following year due to the high wild boar reproductive rates often influenced by density-dependent factors (Servanty et al., 2011; Cappa et al., 2021; Cecchini et al., 2024). This suggests that damage mitigation requires a more multifaceted approach. Targeted numerical control of specific age and/or sex classes, rather than just young individuals, should be combined with non-lethal preventive measures (Cappa et al., 2021; Cecchini et al., 2024). Physical or electric fences are often recommended but, as previously mentioned, can be impractical to implement and costly to maintain. Therefore, their implementation should be preferred on smaller areas and for high-risk crops, such as maize (Bleier et al., 2017; Cappa et al., 2019; Rutten et al., 2020). In some contexts, like in Sweden, the hunting value of wild ungulates can compensate for agricultural damage costs (Menichetti et al., 2019), in turn transforming, if properly managed, conflicts into potential economic opportunities.

4.4 Limitations

This review provides a comprehensive synthesis of studies on wild-domestic ungulate interactions in Europe. However, some limitations warrant discussion. First, the decision to limit the search to English-language literature may have excluded relevant studies published in national languages (e.g., Italian, Spanish, German), which often document conflict dynamics at a local level. However, English is the primary language of international scientific communication and ensures that the summarized data are accessible and comprehensible at an international level. Second, we chose to exclude grey literature. Although this decision may have limited the total number of eligible studies, it was made to include only peer-reviewed evidence to ensure the data robustness. Searching for grey literature is often inefficient in terms of time and resources, and data are rarely collected using systematic methods, thereby making both transparency and replicability of the process challenging (Mahood et al., 2014; Adams et al., 2016).

5 Conclusions

This systematic review evaluated three key aspects of wild-domestic ungulate interactions across Europe: trophic competition,

spatio-temporal interactions, and agricultural damage. These ecological and behavioral interactions frequently manifest as human-wildlife conflicts, and did not emerge as isolated events, but as part of a complex socio-ecological framework that contributes to the vulnerability of agro-livestock systems, particularly in marginal areas. The reviewed literature highlighted a clear bidirectional dynamic: while wild boar and red deer act as primary drivers of conflict by causing significant forage losses and land degradation, livestock husbandry practices and human presence simultaneously exert reciprocal pressure, frequently displacing wild ungulates to suboptimal habitats with potential negative consequences for their fitness.

Despite the observed increasing number of studies in recent decades, the reviewed literature is strongly characterized by a geographic concentration of studies in Italy and a species-specific focus primarily centered on wild boar and red deer, leaning toward the assessment of direct agricultural damage. Consequently, significant research gaps remain, particularly due to the general scarcity of studies investigating trophic competition and spatio-temporal dynamics in most European countries, along with the widespread underrepresentation of alternative wild species such as roe deer, chamois, mouflon, and ibex. Methodologically, standardized monitoring protocols to quantify economic and biomass losses are lacking, thereby limiting the replicability of findings and making results difficult to compare. Finally, the reviewed evidence highlighted that conflict-prone areas are dependent on context and landscape configuration.

To enhance human-wildlife coexistence, applying an integrated management approach is essential. This approach should not only focus on the numerical control of wild populations but also assess the feasibility and implementation of appropriate non-lethal preventive measures to protect crops. Moreover, it should also encourage sustainable livestock husbandry systems to mitigate the disturbing effects of livestock on wildlife. Finally, the implementation of standardized monitoring protocols and the inclusion of farmers in research activities assume paramount importance in enabling robust comparisons and developing effective management strategies to mitigate the human-wildlife conflicts in shared landscapes.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author/s.

Author contributions

LC: Writing – review & editing, Methodology, Data curation, Investigation, Conceptualization, Writing – original draft. MC: Validation, Writing – review & editing, Supervision. SB:

Validation, Methodology, Data curation, Investigation, Supervision, Conceptualization, Writing – review & editing. EP: Validation, Writing – review & editing, Supervision. MF: Investigation, Writing – review & editing, Data curation, Methodology, Validation, Supervision, Conceptualization.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

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