Wild vs. domestic ungulate ecosystem impacts: understanding functional differences requires greater focus on mechanisms

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Abstract:

Ungulates play vital roles in ecological systems, shaping plant biomass and diversity via herbivory and impacting soil properties through trampling and nutrient deposition. As ungulate communities fluctuate across the globe, the extent to which wild ungulates and domestic livestock can play similar ecological roles is an increasingly vital - and fraught - question. Here, we synthesized the literature directly comparing wild and domestic ungulate effects on above- and belowground ecosystem responses to assess the direction and relative strength of species' impacts within shared environments. We then investigated the intrinsic and extrinsic mechanisms researchers identified as driving differences in ecosystem responses to wild and domestic ungulates. Overall, our synthetic review revealed that surprisingly few studies directly compare the effects of wild and domestic ungulates, and even fewer explicitly consider the mechanisms underlying observed outcomes. We found that wild and domestic ungulate effects on plant and soil variables are overwhelmingly similar in kind, differing in intensity rather than direction, with domestic ungulates exhibiting stronger effects on ecosystem responses. Specifically, livestock appear to reduce plant biomass and cover more than wild species, but wild ungulates exhibit more positive effects on plant diversity. Diet and stocking density were by far the most frequently referenced mechanisms explaining differences between wild and

domestic ungulates, and other mechanisms (e.g. behavior, movement, veterinary treatments) were rarely considered, let alone tested explicitly. Thus, more intentional study of the intrinsic and extrinsic factors underlying ungulate effects on ecosystems, and particularly on belowground processes, is necessary for a more complete understanding of the functional interchangeability - or irreplaceability - of wild and domestic ungulates in a rapidly changing world.

Keywords: wild ungulates, livestock, ecosystem functioning, primary productivity, plant diversity, belowground processes, regenerative agriculture, ecological restoration

Introduction:

Large mammalian herbivores, and particularly ungulates, play vital roles in ecological systems and human societies (Pringle et al. 2023). Ungulates, or hoofed mammals, are major food sources for people and non-human predators, and the resources they produce (e.g., hide, fiber, horns) have provided vital materials for clothing, tools, and cultural artifacts for millennia (Pascual-Rico et al. 2021; Velamazán et al. 2020). Beyond providing resources to other consumers, however, ungulates can also exert strong top-down effects on ecosystems. Historically common in many terrestrial biomes, ungulates shape plant biomass and diversity via selective consumption of plant material (Schmitz 2008). Furthermore, ungulates impact soil properties through trampling and nutrient deposition in the form of dung and urine (Bardgett & Wardle 2003; Kitchell et al. 1979). Accordingly, the density and composition of ungulate communities can have important implications for primary productivity, carbon sequestration, fire intensity, and numerous other ecosystem functions.

The ecological and cultural importance of ungulates are exemplified by both wild and domestic species; however, there are key differences in the nature and extent of wild and domestic ungulate impacts on landscapes worldwide (Pringle et al. 2023). Though wild ungulates account for half of all wild mammalian biomass, domestic ungulates are currently far more numerous and widespread, with domestic cattle alone contributing 42 times the biomass of all wild ungulates combined (Greenspoon et al. 2023). As anthropogenic activities have contributed to drastic declines in wild ungulate populations across the globe, animal agriculture has proliferated, such that domestic species have largely displaced wild populations in many regions (Sandom et al. 2014, Ripple et al. 2015). At the same time, some wild ungulates (e.g. deer in suburban North America) have exhibited large population spikes due to the eradication of predators, access to anthropogenic resources such as fertilized crops and fields, and deliberate supplemental feeding by humans (Côté et al. 2004, Jones et al. 2014). These changes in mammalian communities have led to substantial environmental change, even beyond the direct consequences of human habitat alteration, including woody plant encroachment (Bakker et al. 2016), dryland degradation (Asner et al. 2004), and plant species invasions (Averill et al. 2018). As a result, those tasked with managing lands with wild and/or domestic species have had to confront the consequences of ungulate population shifts - whether intentional or accidental - on ecosystem functioning in multi-use landscapes.

Accordingly, the extent to which wild and domestic species can play similar ecological roles is an increasingly vital - and fraught - question. Environmental protection and agricultural production both require effective management of herbivore communities, and the functional similarity - or dissimilarity - of wild and domestic ungulates are invoked by a wide spectrum of stakeholders to support competing policies and land management strategies. Many regenerative agriculture movements are based on the philosophy that, under appropriate management, domestic ungulates can replicate the effects of wild ungulates on ecosystems and enhance desired ecological functions such as carbon sequestration, particularly in landscapes with long histories of herbivory (Kleppel & Frank 2022). Furthermore, some conservation efforts have proposed instrumentalizing such functional redundancy through strategic livestock grazing to promote the restoration of landscapes with extirpated or extinct wild ungulates (Gordon et al.

2021, Kleppel & Frank 2022, Lundgren et al. 2020). Others have argued that livestock species and wild ungulates are fundamentally non-equivalent because wild species often have long coevolutionary histories with vegetation and exhibit unique adaptations to a given landscape (Reinhart et al. 2022). Thus, many conservationists hold that ecological restoration should necessarily entail the promotion of native species and the reduction of animal agriculture, particularly as livestock production often requires more intensive resource exploitation to be profitable in a market economy. Addressing and reconciling these competing perspectives is critical to both conservation and food production under shifting social and environmental conditions.

Evidence in support of each of these arguments can be found (e.g. Price et al. 2022, Lundgren et al. 2024), and it is clear that the extent to which wild and domestic ungulates have similar or distinct impacts on ecosystem functioning is highly scale- and context-dependent. Thus, truly understanding the contexts in which wild ungulates and livestock are ecologically interchangeable - as well as the environmental consequences of species turnover when they are not - necessitates a more thorough investigation of the mechanisms driving ungulate effects on plants and soil (Pringle et al. 2023, Monk 2024). Many of these mediating factors may be traits inherent to specific ungulate species, such as body size (which could influence the type of plants herbivores have access to or the extent of soil trampling; Cumming and Cumming 2003, Trepel et al. 2024, Lundgren et al. 2024), physiological adaptations (which could determine how far herbivores can travel from water sources or what microenvironments they can tolerate; Allred et al. 2011, Sitters et al. 2009), or movement and migration habits (which could mediate seasonality of herbivory or patterns of nutrient deposition on the landscape; Bauer and Hoye 2014, Geremia et al. 2019). When such intrinsic mechanisms differ greatly between species, wild and domestic ungulates are unlikely to act as effective ecological surrogates for one another.

However, many mechanisms that determine the nature of ungulate impacts are extrinsic factors resulting from human management or environmental context rather than intrinsic species traits. Stocking density and grazing intensity determine overall levels of herbivory, influencing plant biomass and cover; similarly, anthropogenic barriers to ungulate movement such as fencing and highways can drive the spatial distribution of herbivory (Boone and Hobbs 2004, Frank et al. 2016, Prokopenko et al. 2017, Wells et al. 2022). Where these factors are largely responsible for the ecological impacts of herbivores, shifts in management strategies could lead to increased functional redundancy between wild and domestic ungulates. Yet despite these nuances, there has hitherto been insufficient synthetic research on the mechanisms and functional traits (beyond species identity) that can generally predict whether wild and domestic ungulates can function as ecological surrogates (Öllerer et al. 2019, Pringle et al. 2023, Schieltz and Rubenstein 2016), or whether such ecological surrogacy can extend beyond effects on aboveground variables to influence belowground plant productivity and soil properties (Andriuzzi and Wall 2017, Pringle et al. 2023).

Here, our overarching goals were to (a) assess whether there are consistent patterns in the relative effects of wild and domestic ungulates on above- and belowground ecosystem responses, and (b) leverage the primary literature to identify the key mechanisms that underlie these observed differences and similarities between domestic and wild ungulates. First, we synthesized the literature directly comparing wild and domestic ungulate effects on ecosystem functions and properties (both above- and belowground) to assess the direction and relative strength of species' impacts within shared environments. We then reviewed the possible mechanisms that can mediate the impacts of distinct ungulate species on vegetation and soil. Finally, we investigated the mechanisms to which these outcomes were attributed across studies, identifying insights and research priorities that emerged as requisite for a more complete understanding of the functional interchangeability - or irreplaceability - of wild and domestic ungulates in a rapidly changing world.

Synthetic Approach:

We systematically reviewed the literature comparing wild and domestic ungulate effects on ecosystems in the Web of Science. We used the terms “("livestock" OR "domestic ungulate*" OR "domestic herbivore*") AND ("wild herbivore*" OR "wild ungulate*" OR "free-ranging herbivore*" OR "free-ranging ungulate*" OR "native ungulate*" OR "native herbivore*") AND ("ecosystem" OR "vegetation" OR "plant community" OR "plant diversity" OR "biomass" OR "NPP" or "soil carbon" OR "soil nutrient*")” to search all document fields to identify publications matching our scope of inquiry in August 2024. This search yielded 821 publications, and after reviewing all titles and abstracts we read full texts of 112 publications that were potentially relevant to our synthetic review. Because not all publications are indexed in Web of Science, we further supplemented this review by searching the above search terms in Google Scholar. We identified 5 additional relevant studies that were not indexed in the Web of Science, resulting in a total of 117 full texts reviewed (Fig. 1).

To meet our inclusion criteria, studies had to a) measure the effects of ungulate species on plant or soil response variables, and b) consider both wild and domestic ungulate species effects within the same ecosystem. Fifty three publications met these criteria for inclusion in our synthesis (Fig. 1). For each included publication, we noted the study location, ungulate species investigated, and treatment structure. We then identified all ecosystem responses to both wild and domestic ungulate treatments measured in each study, and grouped these ecosystem responses into 18 categories of above- and below-ground responses (Fig. 1).

For each response measured in each study, we identified whether the effects of wild and domestic ungulates were determined to be equivalent or distinct (i.e. differences were statistically significant, or effect sizes differed). If the latter, we assessed whether wild or domestic ungulate treatments had greater or smaller values of that response, relative to each other and to any treatment with no herbivores (if applicable; hereafter referred to as “control treatment”). For all studies that compared wild and domestic ungulate treatments to control treatments with no herbivory (i.e. cages, exclosures, or ungulate-free zones on the landscape), we assigned a semi-quantitative, semi-qualitative measure of relative effect size we term a “relative response value” (RRV) for each relevant ecosystem response (Fig. 1). To calculate RRVs, we assigned each measured response a position on a theoretical graph with wild ungulate effects on the x-axis and domestic ungulate effects on the y-axis. Positioning on the graph was determined by a) whether each ungulate treatment’s effects were positive, negative, or neutral (relative to the control treatment) and b) whether wild and domestic ungulate treatments effects were equivalent (i.e. both positive of both negative, and falling along the 1:1 line) or differing in magnitude (i.e. the response variable was significantly greater in the domestic ungulate treatment than in the wild ungulate treatment, and both were greater than the control; Fig. 1). Where wild and domestic ungulate treatments had opposite effects relative to the control, RRVs fell into the upper left or bottom right quadrants (Fig. 1). Finally, we indicate the total number of RRVs in a given position per response type (i.e., weight of evidence for that particular relationship) by indicating the number of RRVs within the circle and proportional to the length of the spoke on the graph (Fig. 1).

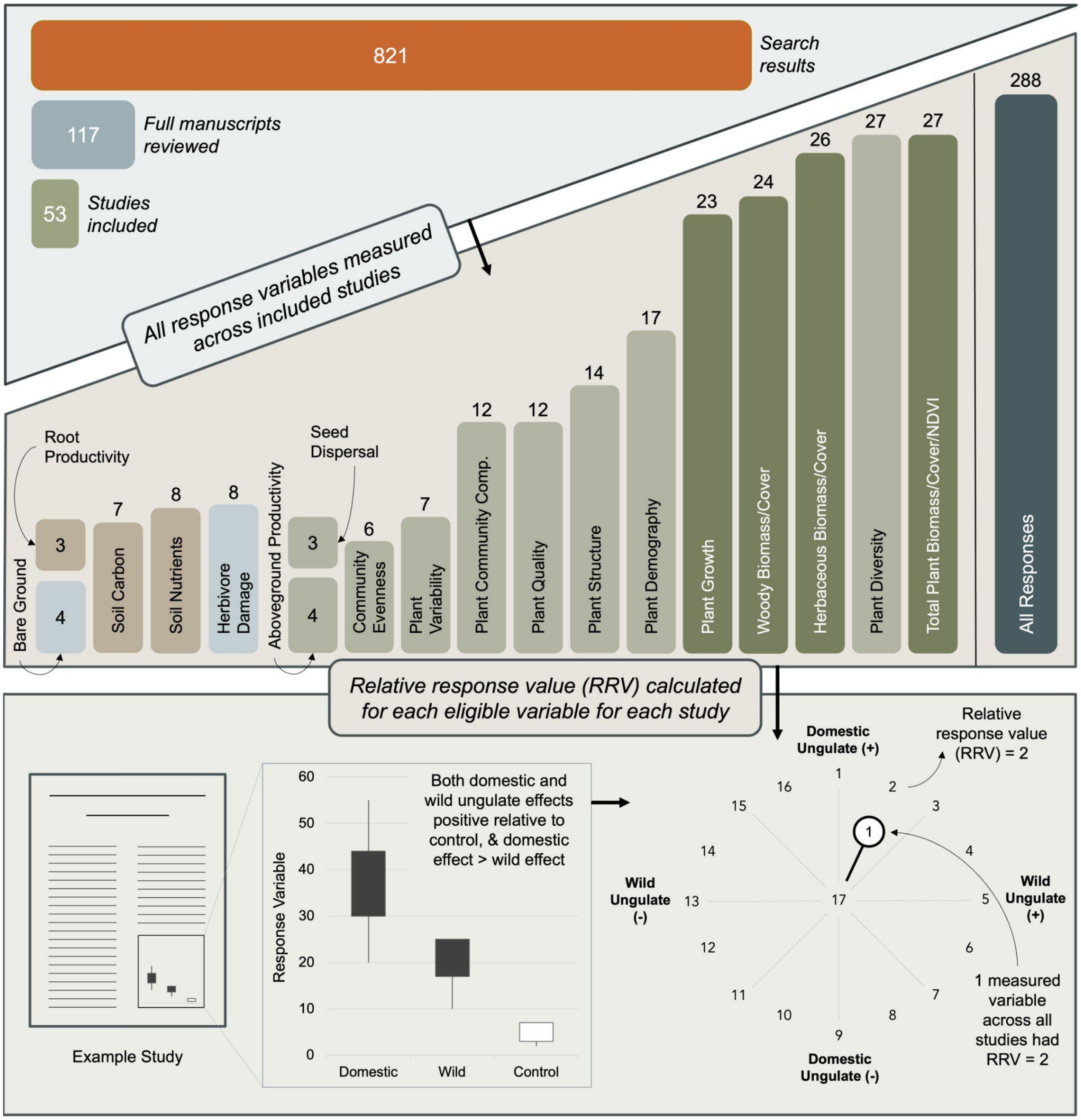
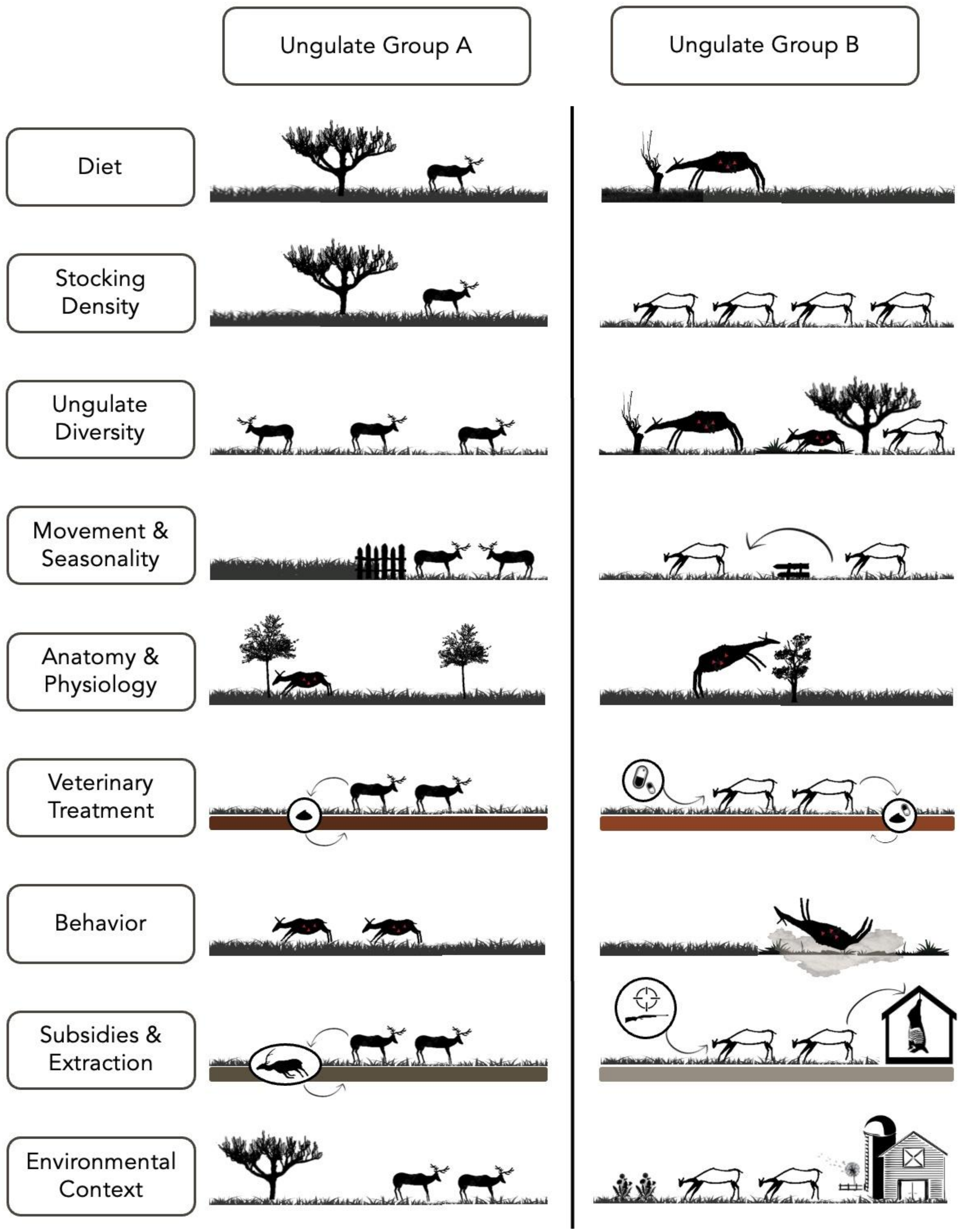


Figure 1. Schematic of our systematic review process. We reviewed 821 abstracts, 117 manuscript full texts, and ultimately identified 53 studies that met our search criteria. We then categorized response variables (dark green = vegetation quantity, light green = vegetation traits, brown = belowground variables, blue = other) and tallied the number of responses of each type measured across all studies. Finally, for studies that included treatments with domestic ungulates, wild ungulates, and ungrazed controls, we assigned a relative response value (RRV) for each response variable to characterize the relationship between domestic ungulate effects (+/-) and wild ungulate effects (+/-) relative to ungrazed controls, and summed and plotted the RRVs for each variable; the length of spokes as well as the number inside the bubble in each RRV figure represents the number of total responses across all studies with that RRV for that category of response variable.

We carefully reviewed all publications to determine the mechanisms researchers identified as drivers of differences between the effects of different groups of ungulates on ecosystem responses. In conducting this review of the literature, we identified nine general categories of these mechanisms: diet, stocking density, diversity of the ungulate community, movement and seasonality, anatomy and physiology, veterinary treatments, behavior, subsidies and extraction, and environmental context (Box 1). Though these categories are neither exhaustive nor mutually exclusive, they seemed to best represent the most commonly identified mechanisms considered in the studies we reviewed. For each included study, we first noted which mechanisms were mentioned or considered at all throughout the text, including in a general sense (e.g. “stocking density can determine the impacts of herbivory by ungulates”). Next, we determined which mechanisms were identified by the manuscript authors as the potential drivers of observed similarities or differences between wild and domestic ungulates in the study (generally in the form of statements in the results, discussion, or conclusion; e.g. “the greater vegetation reduction we observed under domestic ungulate grazing compared to wild ungulate grazing may be due to higher stocking densities in livestock pastures”). Finally, we assessed whether the study presented data that supported these conclusions, or whether the cited mechanisms were only mentioned speculatively, often in the discussion or conclusion sections of the manuscript.

Box 1: Mechanisms that mediate the effects of different ungulate groups on ecosystem functioning



Diet: Many ungulates differ in the identity and range of plant species they consume. Broadly, some ungulates are browsers (consuming parts of woody vegetation such as trees and shrubs) while others are grazers (consuming herbaceous vegetation) or mixed-feeders (a combination of both); landscapes dominated by these different guilds may diverge in their proportions of woody and herbaceous vegetation (Veblen et al. 2015, Seymour et al. 2016). Dietary differences can also be more granular; for example, some ungulates may prefer just a few dominant palatable species (which can reduce dominance and increase plant diversity) while others are more generalist grazers (particularly when ungulate densities are high or resources are scarce) (Ratajczak et al. 2022).

Stocking Density: The effects of different ungulate species on vegetation and soil is often influenced by stocking density, or the number of individuals of that species within a given area grazing during a period of time. Higher stocking densities of certain species can lead to greater removal of preferred forage plants, or greater trampling and compaction of the soil in areas where they congregate; in turn, low stocking densities in ecosystems adapted to herbivory can decrease plant diversity or reduce productivity (Riginos et al. 2018, Porensky et al. 2020, Stanley et al. 2024). Appropriate stocking densities may promote biodiversity and productivity by regulating competition and triggering compensatory growth.

Diversity of the Ungulate Community: Even when stocking densities are comparable, the species diversity of distinct ungulate communities can determine the nature and strength of their effects on ecosystem properties. Increasing diversity in ungulate communities can be positively related to vegetation diversity and ecosystem multifunctionality (Wang et al. 2019; Baumgartner et al. 2015; Velado-Alonso et al. 2020), whereas single-species agglomerations may lead to more intense effects on a few preferred forage species. However, the combined effects of multiple ungulate species on vegetation composition can alternatively be compensatory, leading to overall neutral effects on plant community composition or cover (Baumgartner et al. 2015).

Movement & Seasonality: The distribution of different ungulate species across space and time can mediate their impacts on the landscape. More mobile or wide-ranging species may have more diffuse effects on plants and soils, whereas species that are concentrated in smaller zones (e.g. those constrained by fencing or roads) may generate stronger and more centralized effects (Burgi et al. 2012, Kanga et al. 2013). For example, some ungulate engage in “green wave surfing”, or migrations to follow new vegetation growth, which can often minimize their influence on plant biomass or cover or even promote productivity by concentrating herbivory early in the growing season, whereas more sedentary ungulates may cause greater reductions in plant biomass by continuing to graze vegetation late in the season when there is less opportunity for regrowth (Merkle et al. 2016, Geremia et al. 2019).

Anatomy & Physiology: Intrinsic anatomical and physiological traits mediate herbivore interactions with their environment. Body size determines the plant species and plant parts that ungulates have access to, which can impact species diversity and plant architecture (Stuart-Hill 1992, Trepel et al. 2024); both body weight and foot anatomy (i.e. hard hooves vs. soft foot pads) determine the intensity of herbivore trampling (Schroeder et al. 2022). Similarly, ungulates’ digestive fermentation types, combined with body size, drive the quantity and quality of vegetation consumed, the efficiency of nutrient processing, and the composition of herbivore wastes (Esmaeili et al., 2021; Hopcraft et al., 2012). Digestive traits also influence the viability of seeds processed by herbivores, driving differences in ungulate-mediated plant dispersal (Cappa et al. 2022). Furthermore, some ungulates have physiological adaptations to minimize reliance on surface water, including reduced water loss or the ability to survive on preformed water contained in food (Cain III et al., 2006), while others may be more dependent on surface water, resulting in intensified herbivory near water sources (Sitters et al., 2009).

Veterinary Treatment: The use of veterinary medicine is a key factor distinguishing managed and unmanaged ungulate populations. Beyond impacts on ungulate population densities (Oesterheld 1992), the use of antibiotics and antiparasitics specifically have documented effects on a variety of ecosystem processes (Wepking et al. 2019, Keesing et al. 2013). For example, 40-90% of administered antibiotics may be transferred through the ungulate gut to the environment via the excretion of dung and urine (Sarmah et al. 2006). Higher environmental antibiotic concentrations resulting from this transfer can shift microbial community composition (Wepking et al. 2019, Roy et al. 2023), in turn altering decomposition rates and terrestrial elemental cycling (Schimel and Schaeffer 2012, Wepking et al. 2017).

Behavior: Behavioral differences between ungulate species may lead to divergent impacts on the environment. Some ungulate species create physical disturbances to vegetation (e.g. toppling trees; Sitters et al. 2020) and soil (e.g. wallowing and dust bathing; McMillan et al. 2011). Species may also exhibit highly specific defecation and urination behaviors; for example, vicuñas create latrines to maintain social group cohesion, concentrating nutrients in ways that ungulates with more dispersed defecation patterns do not (Monk et al., 2024). Distinct foraging behaviors can further generate differences in the effects of herbivory on primary productivity or vegetation cover even when ungulate diets are similar (i.e. biting off grass leaves vs. pulling up entire grass tussocks; Schroeder et al. 2022).

Subsidies & Extraction: Human management of both domestic and wild animal populations involves the subsidy and extraction of resources. Resources are supplemented to an ecosystem when ungulate populations are provisioned with food and water (i.e. feed in agricultural or game settings, or artificial water sources in pastures and wild desert areas; Jones et al. 2014, Glass et al. 2022). As a corollary, resources are extracted when individuals are sold, slaughtered, or hunted (Abraham et al. 2021); when dung is collected or redistributed with animals (Augustine 2003); or when horn, fiber, or dairy products are harvested (Carmanchahi et al. 2015, Maher et al. 2023). This import and export of resources to domestic and wild ungulate populations can decouple them from density-dependent ecosystem feedbacks and disrupt their roles in vegetation regulation or nutrient recycling (Brodie and McIntyre 2019, Abraham et al. 2023a).

Environmental Context: Occasionally, different ungulate species may themselves exert similar effects on ecosystem properties, but the contexts in which those ungulates occur are associated with other distinct disturbances or management practices (Navarro et al. 2023). For example, some species may be found closer to human settlements (either because they are domestic species, or because they have adapted to live in close proximity to humans); in these cases, these ungulates may be associated with environmental impacts (e.g. introduced plant species, deforestation) that are not caused by the activities of the ungulates themselves, but rather the environmental contexts in which they are found (in comparison to the habitat of a different species that is constrained to sites with lower anthropogenic impacts; Jones et al. 2014, Li et al. 2022). Analogously, studies carried out under climatically anomalous periods may result in stronger responses than if such conditions were closer to historic climatic patterns. For example, the effect of ungulate grazing under extreme drought may differ greatly from effects recorded during dry years.

Results and Discussion

1. Wild and domestic ungulates affect ecosystems in similar ways, but at different intensities

Across 288 responses from 53 studies, 55% of ecosystem responses differed significantly in the presence of wild vs. domestic ungulates. However, it was very rare for wild and domestic ungulates to have opposite effects on any given ecosystem response; indeed, only 3% of the RRVs we calculated revealed such opposite effects (i.e., instances where one ungulate group was associated with increases in a response relative to ungulate-free controls, while the other ungulate group was associated with decreases in that response; Fig. 2). Thus, wild and domestic ungulate effects on plant and soil variables are overwhelmingly similar in kind, differing in intensity rather than direction in almost all cases we studied. There were, however, marked patterns in the intensity of these effects. Domestic ungulates were twice as likely to have stronger (more negative or more positive) effects on ecosystem responses compared to wild ungulates than the converse (35% of RRVs vs. 17% of RRVs). Domestic ungulates were also more likely to have significant effects on ecosystem responses than wild species, which had no measurable effects for 58% of RRVs. Thus, all ungulates had variable effects on ecosystem functioning (Fig. 2), and wild and domestic species tended to have effects in similar directions but of different magnitude on environmental responses, with domestic ungulates exerting stronger effects than wild ungulates.

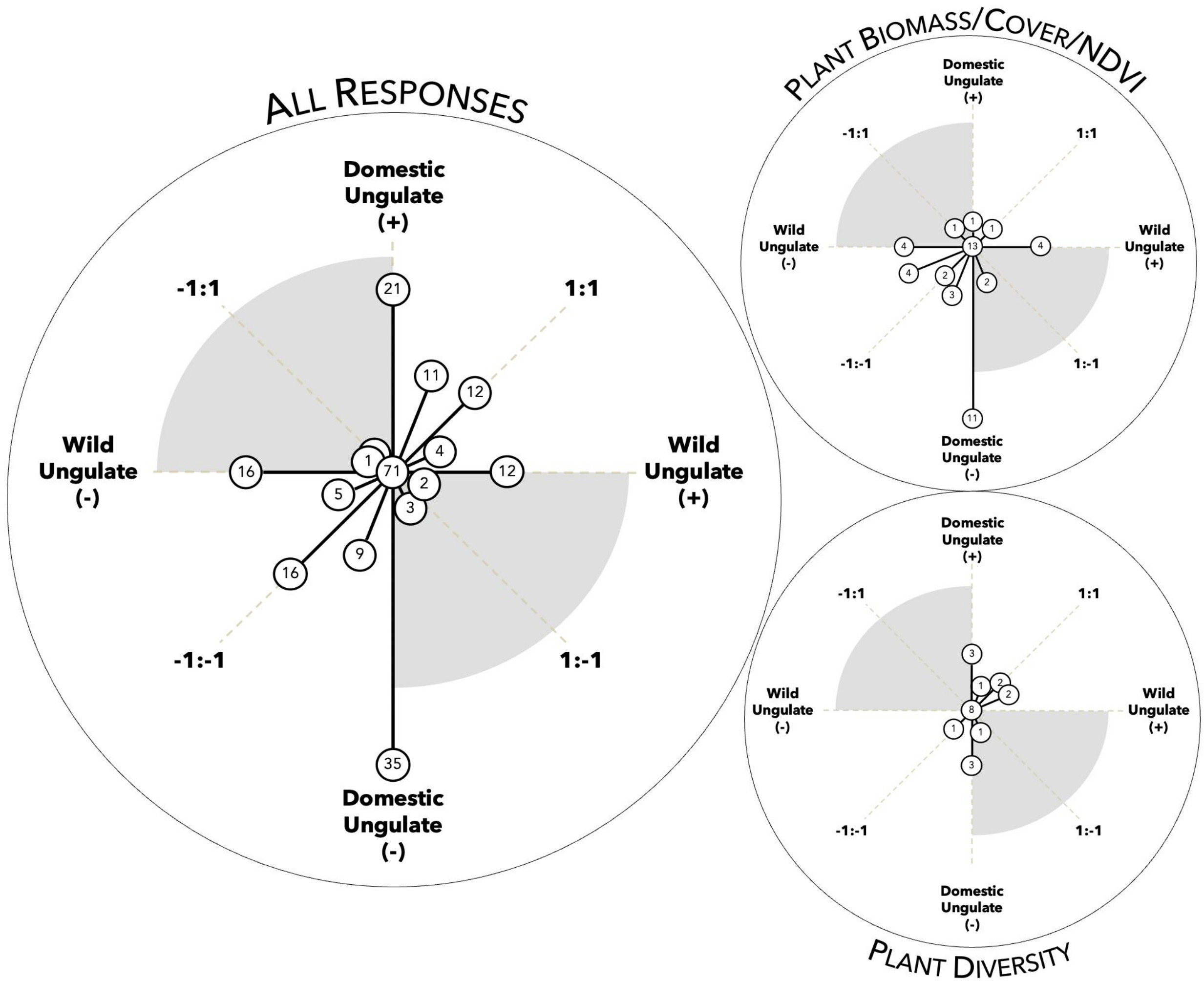


Figure 2. Relationships between wild and domestic ungulate effects (relative to ungrazed controls) on all applicable response variables (left graph), variables related to vegetation quantity (plant biomass/cover/NDVI, top right graph), and metrics of plant diversity (bottom right graph) among studies included in our review. The x-axis represents whether wild ungulates had positive, neutral, or negative effects on a given response variable, while the y-axis represents the directional effects of domestic ungulates. Placement along the 1:1 line reflects statistically similar effects of wild and domestic ungulates relative to ungrazed controls. Positioning in the upper left or bottom right quadrants of each graph denotes opposite effects of wild and domestic ungulates (i.e., one group had positive effects while the other had negative effects; shaded quadrants). Numbers in circles and the length of connector lines denote the number of RRVs with a given relationship across our review.

Upon examining different types of ecosystem responses, however, the nature of wild and domestic ungulate impacts on certain ecosystem functions diverged more. Overall aboveground vegetation metrics (e.g. plant biomass, plant cover, and Normalized Difference

Vegetation Index [NDVI]) responded variably to both groups of ungulates; though all ungulates generally reduced overall vegetation, domestic ungulates were more likely to induce such decreases than wild ungulates (Fig. 2). As a result, most studies found that sites or plots dominated by wild ungulates had greater plant biomass or cover than plots or sites with domestic ungulates (Fig. 3). On the other hand, though domestic ungulates had both positive and negative effects on plant diversity and evenness, wild species had almost universally positive or neutral impacts on diversity, and plots with wild ungulate presence tended to have higher plant diversity than plots with domestic ungulates (Fig. 2, Fig. 3). Accordingly, shifts in ungulate communities as a result of changing land use may more consistently affect the diversity and composition of plant communities than overall aboveground plant biomass, with potential cascading effects on other herbivores and biogeochemical cycling (Afonso et al. 2024, Baidya 2022, Chen et al. 2024).

Most other variables were investigated by too few studies to allow us to draw strong conclusions (Fig. 1); nevertheless, initial trends provide some insight into the ecosystem functions and properties that may diverge most under different ungulate regimes. Based on the few studies that measured these responses, areas with domestic ungulates tended to have more bare ground and higher aboveground productivity; domestic ungulates also appeared to be more effective seed dispersers than wild ungulates (Fig. 3), potentially due to differential consumption of seeds or differences in digestive anatomy that improve viability in seeds passed through domestic ungulate guts (Ansley et al., 2017; Bartuszevige & Endress, 2008; Cappa et al., 2022). In contrast, areas with wild ungulates had greater belowground (root) productivity and soil carbon content compared to domestic ungulate treatments in almost all studies that investigated these belowground responses (Fig. 3). Thus, though wild and domestic ungulates appeared to have similar impacts on many ecosystem responses, domestic ungulate presence may tend to stimulate aboveground productivity while lowering standing biomass, while wild ungulate presence may promote plant diversity, belowground productivity, and potentially carbon sequestration (though research on these latter processes is scant).

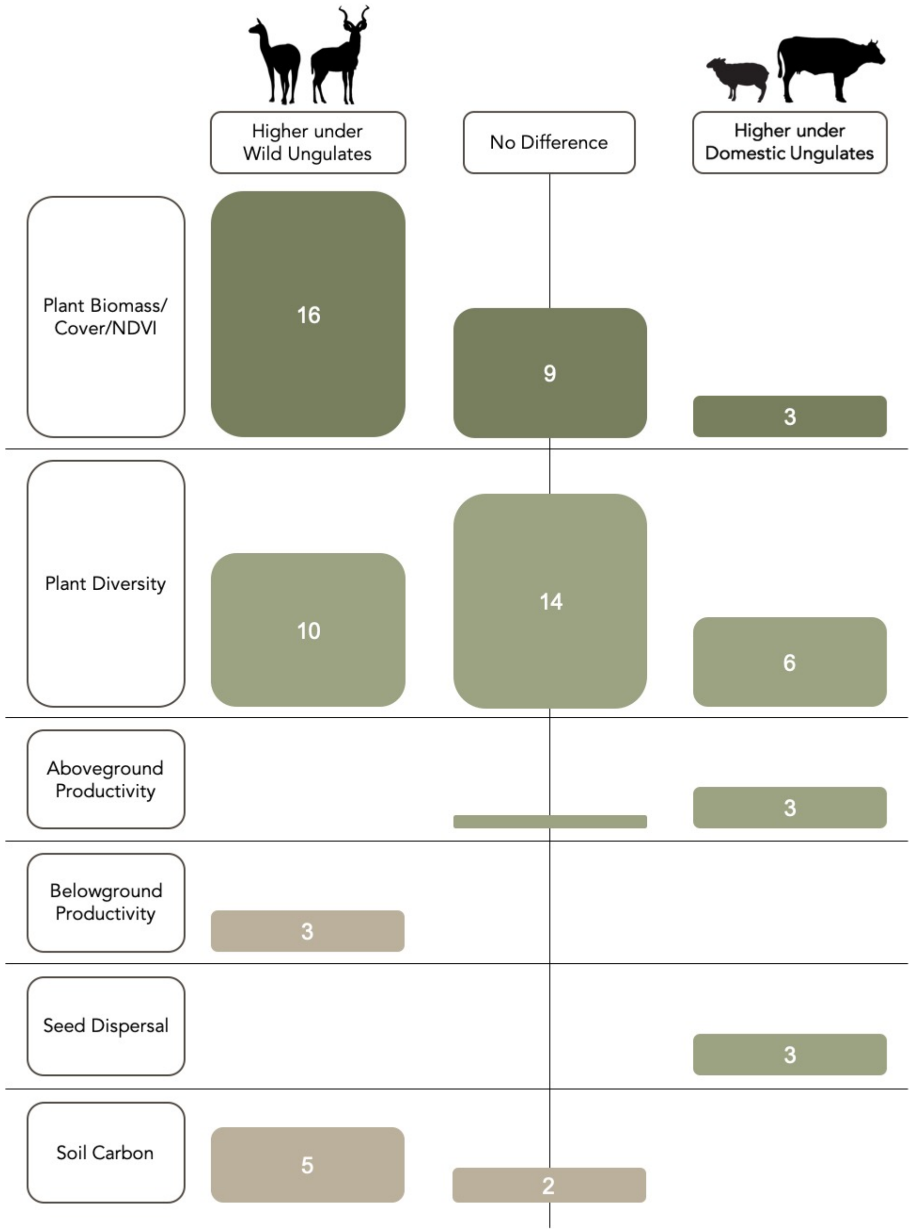


Figure 3. Patterns in relative ecosystem responses to wild and domestic ungulates. Box size and inscribed numbers denote, for each category of ecosystem response, the number of responses across all studies in our review that exhibited higher values under wild ungulates, no difference between wild and domestic ungulate treatments, or higher values under domestic ungulates. Though data were scarce for most ecosystem responses, studies generally reported higher or similar plant biomass, diversity, soil carbon, and belowground productivity in the presence of wild ungulates compared to domestic ungulates, and greater aboveground productivity and seed dispersal in the presence of domestic ungulates.

2. Mechanistic understanding of the differences between wild and domestic ungulate impacts is lacking

Discerning the mechanisms underlying these trends proved a challenging endeavor. Diet and stocking density were by far the most frequently considered mechanisms driving differences between wild and domestic ungulate effects on ecosystems; accordingly, these two mechanisms were also the most commonly attributed causes of observed differences, with more than 75% of studies that considered these two factors determining they played a role in the study's outcomes (Fig. 4). It is perhaps unsurprising that diet and stocking density emerged as the most commonly cited mechanisms underlying differences in ecosystem responses to distinct ungulate groups. Differences in diet are among the most widely documented intrinsic differences between distinct herbivore species, and shifts in dominant herbivore populations play an important role in determining plant community composition and diversity (Kartzinel et al. 2015; Orr et al. 2022). Similarly, stocking density (as well as stocking rate, a related but non-equivalent measure of herbivory intensity over a given time and area) is widely considered an important extrinsic mechanism determining the impacts of herbivores on ecosystems. The number of ungulates in a given area clearly influences rates of vegetation removal, potential compensatory regrowth, and intensity of physical disturbance to plants and soils (Wells et al. 2022, Stanley et al. 2024). Additionally, the density of herbivores as well as the frequency and duration of their presence on a landscape is a commonly emphasized point of intervention where management can mediate ungulate impacts on ecosystem functioning.

Domestic ungulate treatments were often described as having higher stocking densities than wild ungulate treatments, which could partially explain the greater strength of their effects, particularly on plant biomass and cover (e.g. Charles et al. 2016, Giralt-Rueda and Santamaria 2021, Smith et al. 2020, Wasiolka and Blaum 2011; Table S1). Conversely, many studies that found no significant differences between wild and domestic ungulates, or found negligible effects of ungulates on ecosystem responses compared to fenced controls, noted that stocking densities in domestic ungulate treatments were low (Brockaway and Lewis 2003, Cappa et al. 2022, Connell et al. 2018, LaMalfa et al. 2021, Navarro et al. 2023; Table S1). These observations suggest that management strategies can indeed successfully reduce the impacts of domestic ungulates on plants and soils, and that less intensive and industrialized forms of animal agriculture (such as traditional pastoral practices) can more effectively support ecosystem functioning (Velamazán et al. 2023, López-Sánchez et al. 2021, Perea et al. 2016, Munkhzul et al. 2021). However, some experimental treatments may not have accurately reflected realistic agricultural stocking densities for the region, underestimating the strength of domestic ungulate effects (Young et al. 2013). Furthermore, though data on stocking rate/density were frequently available (Fig. 4), studies rarely manipulated stocking density within an ungulate group, obscuring the ways in which stocking density may interact with other key mechanisms and particularly diet. At higher stocking rates, herbivores frequently reduce diet selectivity as competition for plant resources increases (Caram et al. 2024, Stewart et al. 2011). Accordingly, reported results may not reflect the plasticity in ungulate diet that can emerge under fluctuating resource availability and competition, further obscuring the extent to which intrinsic traits or extrinsic management strategies determine the impacts of wild and domestic ungulates.

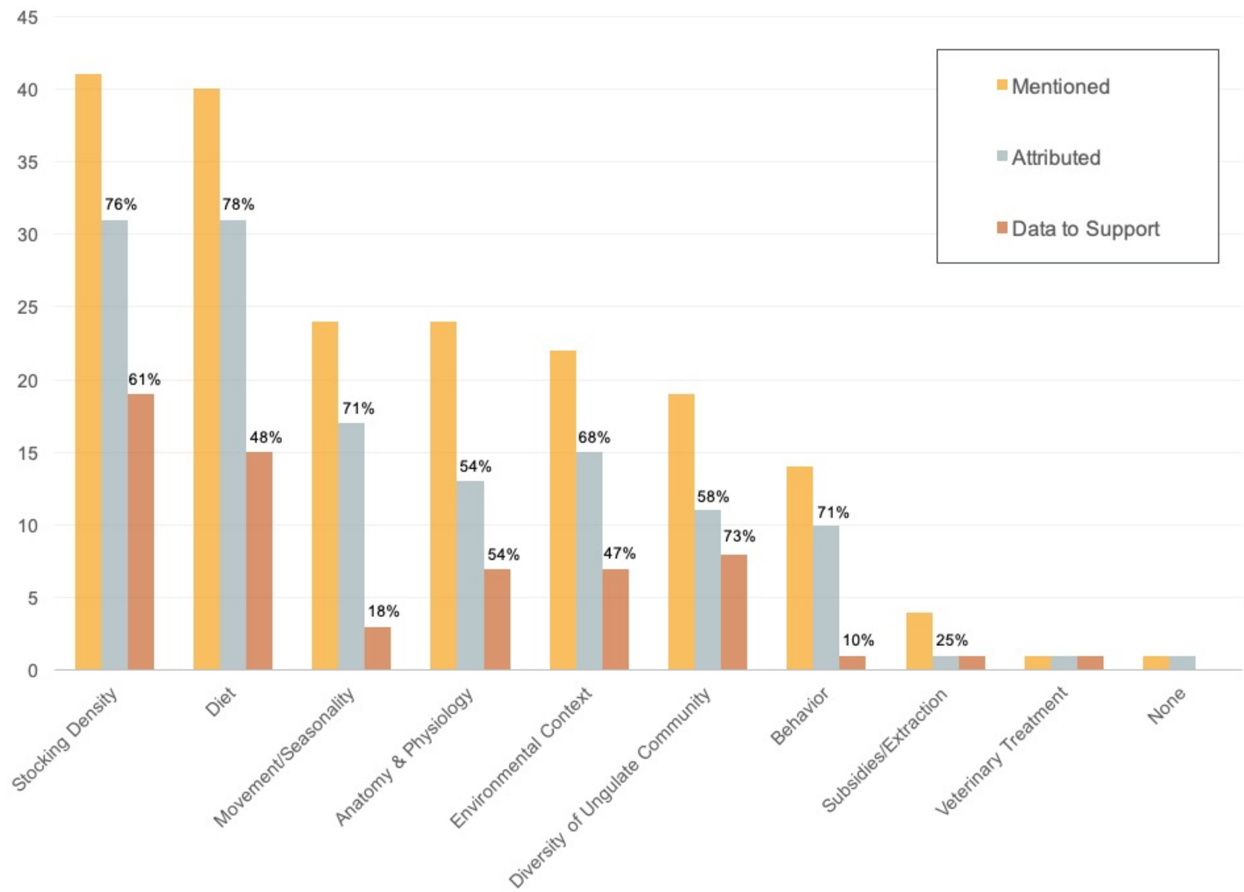


Figure 4. Evidence supporting potential mechanisms underlying differences between wild and domestic ungulate effects on ecosystem responses (See Box 1). Bars denote the number of studies that mentioned or considered a given mechanism in a general sense (yellow), attributed their specific results to that mechanism (blue), and had data to support their attribution to that mechanism (orange). Percentages above bars denote the proportion of studies in the previous category (i.e. 'Mentioned' or 'Attributed') that bar's height represents (e.g. 76% of studies that mentioned or considered stocking density as a mechanism attributed their results to differences in stocking density, and 61% of studies that attributed results to differences in stocking density had data to support that conclusion).

Our results certainly reaffirm the importance of considering both diet and stocking density in investigations of ungulate effects on ecosystems, and greater consideration of the interactions between these and other key mechanisms is necessary. However, our review also highlights the extent to which most other mechanisms we identified are rarely even considered as potential drivers of observed differences between wild and domestic ungulate treatments. Behavioral differences, resource subsidies and extractions, and veterinary treatments in particular were considered by fewer than ⅓ of all studies. Indeed, subsidies and extraction were mentioned as potential considerations in only four studies, and veterinary treatment was identified as a major driver of decreases in soil carbon in the presence of domestic ungulates in the sole study in our review that evaluated this mechanism (Roy et al. 2023). These two mechanisms in particular are extrinsic factors directly impacted by human management of both domestic and wild populations, suggesting that further investigation of these factors could provide important insights into the interactions between ungulate species, management strategies, and ecosystem outcomes. We were unable to identify clear associations between individual mechanisms and specific ecosystem responses, partly due to the apparently haphazard consideration of mechanism in general in studies of wild and domestic ungulates and ecosystem functioning. Moreover, researchers often provided no data to support the mechanisms they cited as potential drivers of their results, instead mentioning these mechanisms in a more speculative fashion in the discussion and conclusion sections of manuscripts (Fig. 4). Thus, our ability to draw conclusions about specific mechanisms and their interactions explaining responses to wild and domestic ungulate grazing is limited. There is an urgent need for studies directly comparing ungulate types that test the specific mechanisms behind these more general responses.

3. Limitations and biases in the existing literature

Limitations in geographic diversity and treatment structure among included studies restrict the scope of our conclusions. Notably, many treatment structures did not allow for the effective isolation of differences between domestic and wild species (Fig. 5). For example, some studies' designs could not exclude wild ungulate presence, so domestic ungulate treatments measured the additive effects of wild and domestic species - potentially overrepresenting the perceived impacts of domestic livestock on plants and soil (Fig. 5). This treatment structure is perhaps more biologically realistic than studies that completely isolated the effects of domestic and wild ungulates, as managed and free-ranging ungulate populations share landscapes and resources in many parts of the world. Nevertheless, failures to completely isolate the effects of these ungulate groups limit our understanding of whether their differential impacts are due to intrinsic differences between species or the overall pressures of greater ungulate densities.

Furthermore, as is the case with many systematic reviews and meta-analyses, the studies included in our synthesis were overwhelmingly located in North America and East Africa, where colonial legacies have historically concentrated Western academic ecological research (Fig. 5; Martin et al. 2012). Indeed, because the Kenya Long-Term Exclosure Experiment (KLEE) is among the most long-standing and productive manipulations of wild and domestic ungulate presence in situ (Goheen et al. 2018), 28% of our final studies were conducted within KLEE. Accordingly, many of the results presented here reflect the impacts of wild and domestic ungulates on ecosystem functioning in one particular region of Kenya. Further comparative study of the effects of wild and domestic ungulates on plants and soils, and more systematic evaluation of the mechanisms driving these outcomes, is necessary to provide a more reliable portrait of functional redundancy between different ungulate groups under shifting management strategies and environmental pressures.

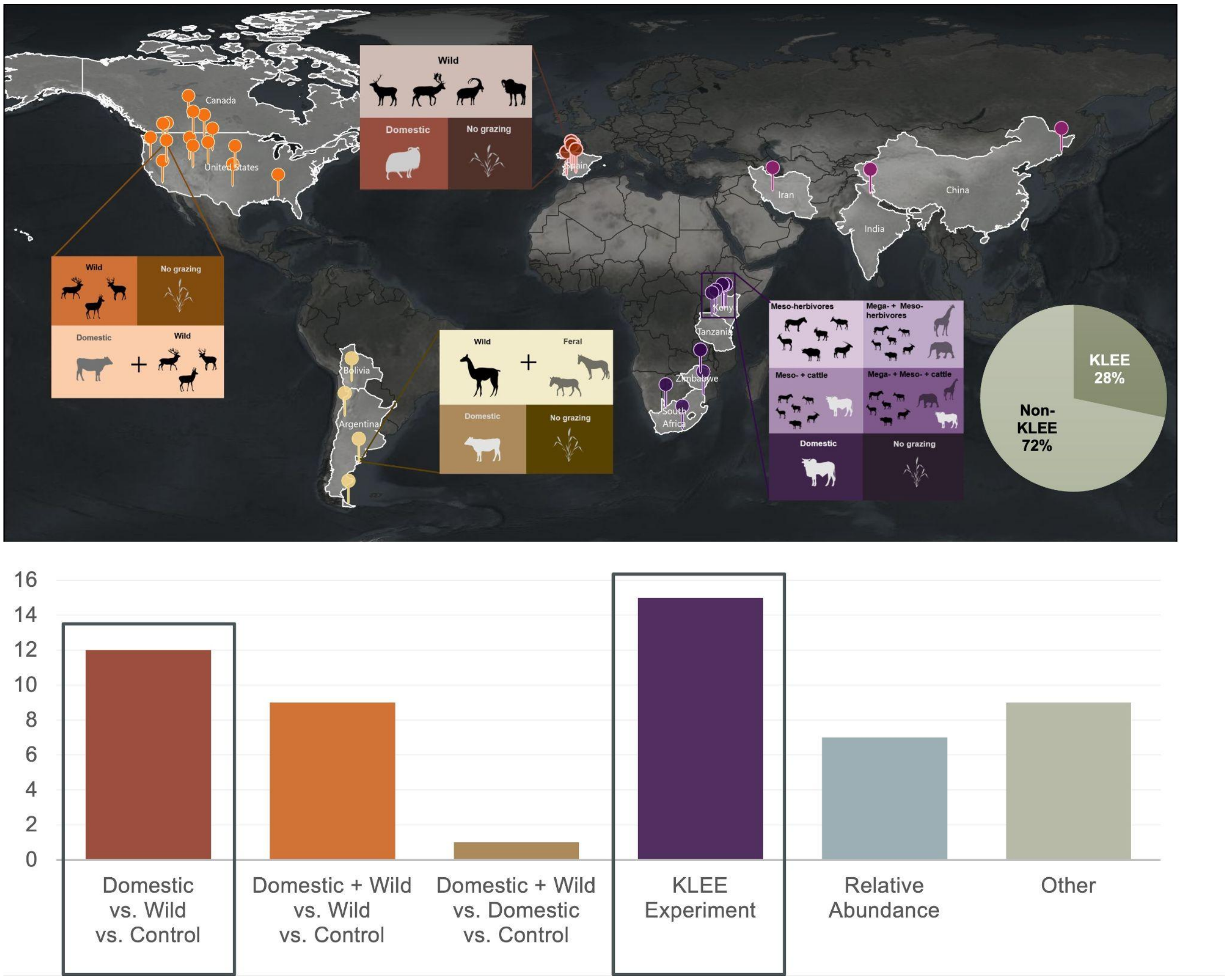


Figure 5. Global distribution of studies included in our review and their experimental treatment structures. a) Geographic locations of studies included in our systematic review; pins denote exact study coordinates while countries are highlighted in white. Insets represent example treatment structures; pie chart insert demonstrates the proportion of studies in our review that were part of the Kenya Long-term Exclosure Experiment (KLEE), highlighted in the adjacent purple inset. b) Number of studies in our review that applied each treatment structure to disentangle the ecological effects of wild vs. domestic ungulates (various combinations of wild ungulate grazing, domestic ungulate grazing, and an ungrazed control; the KLEE experiment that also controlled for wild ungulate body size; non-experimental estimates of relative abundance of each ungulate group; or some other method). Bars circled in black denote the only treatment structures that explicitly measure the effects of domestic vs. wild ungulates in isolation in addition to an ungulate-free control treatment.

Future Directions and Conclusions

Overall, our synthetic review revealed that surprisingly few studies directly compare the effects of wild and domestic ungulates on plant and soil response variables (Fig. 1, Fig. 5, Table S1). Even fewer explicitly consider the mechanisms underlying similarities and differences in wild and domestic ungulate effects on ecosystems (Fig. 4) and we found no studies testing hypotheses about interacting mechanisms. Plant biomass or cover and plant diversity were the most commonly studied ecosystem response variables (Fig. 1), and diet and stocking density were the mechanisms most frequently considered and to which most differences between wild and domestic ungulate impacts were attributed (Fig. 4) Though data were scant overall, domestic ungulates tended to have similar, but stronger, effects on ecosystem responses compared to wild ungulates. Trends in our results point to fruitful avenues of future research, and our review highlighted several important knowledge gaps that stood out as clear priority areas (Table 1).

Table 1. Testable hypotheses and research approaches regarding mechanisms underlying differences in ecosystem responses to wild and domestic ungulates.

Example Hypothesis	Research Approach
Stocking density interacts with ungulate species dietary preference to mediate ungulate impacts on plant diversity	Experimental variation of stocking density of domestic and/or captive wild ungulates or comparison of sites with natural variation in stocking density, coupled with fecal dietary analyses and surveys of plant diversity across ungulate treatments
Ungulate feeding behavior (i.e. clipping off grass leaves with teeth vs. pulling up plants from the root) drives differences in biomass and above- and belowground productivity in areas with wild species vs. domestic livestock	Simulation of feeding behaviors (i.e. experimentally cutting vegetation vs. pulling up vegetation) in exclosed plots; comparison of biomass and productivity in experimental plots to sites representative of each land use type on the landscape
Wild and domestic ungulates will elicit more similar ecosystem responses when ungulate groups have greater shared evolutionary histories and/or anatomical and physiological traits	Comparison of the effect size of ungulate species on ecosystem responses under experimental conditions with same domestic species, but different wild ungulates, in settings where the two ungulate guilds are closely related or share similar traits (e.g. body size, hoof anatomy, fermentation mode) and in settings where they are distinct
Increasing aridity and drought will increase competition for resources, reducing diet selectivity and intensifying the effects of both wild and domestic ungulates on plant biomass and diversity	Assessment of plant biomass and diversity in areas with similar ungulate densities and plant communities but differing exposure to drought
Constraining wild ungulate movement via habitat fragmentation or disruption of migration patterns will replicate domestic ungulate impacts on vegetation and soil in smaller pastures	Measurement of intensity of herbivory, soil compaction, nutrient availability, and other ecosystem responses along a gradient of protected areas of different sizes, but with similar ungulate species composition; case-control comparison of these metrics between sites with undisturbed movement pathways and sites before and after a major disruption to ungulate connectivity

1. Belowground ecosystem functioning remains a key knowledge gap

There is an urgent need for greater understanding of ungulate impacts on belowground ecosystem functioning. Only a few studies compared the effects of wild and domestic ungulates on belowground properties (e.g. root biomass or productivity, soil carbon, soil nutrients, or microbial community composition). Among the few studies that investigated the effects of ungulate groups on soil carbon, sites with wild ungulates tended to have greater soil carbon content than sites with domestic ungulates (Molaeinasab et al., 2018; Roy et al., 2023; Sitters et al., 2020; Fig. 3). This could be due more to the impacts of long-term land use associated with human presence and animal agriculture than the activity of the ungulates themselves. For example, one study comparing different trans-Himalayan valleys in India found that exclusion of large herbivores did not impact soil carbon compared to adjacent plots in either land use type, but valleys with wild ungulates had overall greater soil carbon content than valleys dominated by domestic livestock (Bagchi & Ritchie, 2010b). However, research from this study system also revealed that wild ungulate herbivory tends to promote greater root productivity than domestic ungulate herbivory, which could explain differences in carbon content as much soil carbon is derived from living root inputs (Sokol et al. 2019, Roy et al. 2023, Bagchi & Ritchie 2010a, b). Such contrasts highlight the necessity of greater investment in understanding the intrinsic and extrinsic mechanisms underlying these impacts. There is a growing interest in the conservation, sustainable development, and finance sectors in the role both wild and domestic herbivores could play in mediating carbon sequestration, particularly in grasslands where the majority of carbon is stored belowground (Kristensen et al. 2022, Borer and Risch, 2024, Stanley et al., 2024). Many producers and researchers have touted the potential benefits of carefully managed domestic livestock for soil fertility, carbon sequestration, and overall grassland health (Whitehead 2020, Gordon et al. 2021, Prairie et al. 2023), and conservation entities are also banking on the potential for wild ungulates to impact soil carbon by selling carbon credits for biodiversity preservation (Benghazi et al. 2022, Duvall et al. 2024). These projects are advancing at paces outstripping ecological knowledge underlying such claims, as is often the case when decision makers are necessarily tasked with rapidly addressing acute socio-ecological challenges with limited information. Nevertheless, the scale of these investments–

coupled with the high stakes for both human and non-human communities–renders increased understanding of the impacts of diverse ungulate species on belowground ecosystem functioning, and especially carbon cycling, ever more urgent (Duvall et al. 2024, Borer and Risch 2024).

2. Towards a mechanistic understanding of ecosystem responses to wild and domestic ungulates

Few studies explicitly tested mechanisms driving trends in ecosystem responses to wild and domestic ungulate presence (Fig. 4). Most mechanisms beyond differences in diet and stocking density were rarely considered and almost never directly investigated (Fig. 4). The roles of extrinsic mechanisms such as anthropogenic subsidies and extraction (i.e. supplemental feeding to maintain higher ungulate populations or population culling) and veterinary treatment, in particular, were largely uninvestigated. Yet these mechanisms are among the most direct ways management influences herbivore populations, and each have separately been shown to influence herbivory pressure and biogeochemical cycling (Abraham et al. 2023a, b, Ferraro & Hirst 2024). Despite this lack of mechanistic testing or comprehensive consideration of diverse mechanisms, ungulate species identity and livestock management practices were both frequently cited as causes of observed patterns, exemplifying a common tendency in ecology to infer causation in the absence of concrete evidence (Fig. 4, Addicott et al. 2022).

Systematic investigation not only of the initial trends we detected in vegetation and soil responses to ungulate presence, but the extrinsic and intrinsic drivers underlying them, will be vital for determining the extent to which wild and domestic ungulates play fundamentally distinct roles in ecosystem functioning or whether management strategies can influence their functional redundancy. For example, based on the very limited research comparing above- and belowground productivity under wild and domestic ungulate herbivory, it seems that domestic ungulates may be more likely to stimulate aboveground productivity and wild ungulates may be more likely to promote belowground productivity (Fig. 3). The differential responses of productivity to wild and domestic ungulates could be a reflection of intrinsic dietary preferences driving shifts in plant species composition. Specifically, wild ungulate herbivory could promote belowground productivity by selecting for species with high root:shoot ratios (Roy et al. 2023, Bagchi and Ritchie 2010a). Alternatively, ungulate feeding behaviors (another intrinsic mechanism) could underlie these differences, as when wild species clip grass leaves and preserve root mass, while domestic species pull up vegetation and disrupt belowground productivity (Schroeder et al. 2022). However, these patterns could also be due to extrinsic factors, such as an increased prevalence of annual plant species in agricultural contexts, either due to deliberate seeding for forage or inadvertent transport by livestock and humans (Rinella et al. 2012, Daijun et al. 2023). Fast-growing, annual plants may exhibit higher investment in aboveground productivity following grazing; in this case, the environmental context associated with livestock, rather than their inherent species traits, would drive their impacts on primary productivity (Díaz et al. 2007). Such examples highlight the importance of testing diverse mechanisms, as well as the interactions between mechanisms such as diet and stocking density, in an effort to understand how ecological processes will respond to land use change and ungulate population fluxes.

3. Expanding geographical and methodological scopes

Teasing apart global patterns in ecosystem responses to wild and domestic ungulates requires greater geographic and methodological variation. Like most global syntheses, we found that most studies were concentrated in just a few countries and long-term study sites (Fig. 5; Martin et al. 2012). Expansion of mechanistic research to more diverse regions of the world will expand insights to places where the majority of human communities are balancing reliance on animal agriculture with wildlife preservation and climate change mitigation needs. Additionally, expanding the distribution of studies will allow for a greater understanding of how environmental context and intrinsic animal traits operate as mechanisms underlying apparent differences. For example, investigating the effects of one domestic species (e.g. cattle) on plant communities with similar abiotic conditions but different levels of adaptation to bovine grazers (e.g. east African savannas, where cattle were domesticated, vs. South American savannas, where cervids are the largest native ungulates) could shed light on the relative roles of climate, management, and coevolution of plant and herbivore traits in driving plant responses to herbivory (Table 1). Furthermore, though exclosure studies are crucial for determining causality and experimentally manipulating herbivore presence, such studies should be supplemented by landscape-scale observational research to verify that results apply at scale. Studies that applied such multi-scale approaches found that some patterns held at the landscape level, but others did not perfectly map onto differences between grazed and ungrazed experimental plots at smaller scales (Bakker et al. 2016, Hempson et al. 2017, Roy et al. 2023). This is potentially because these experiments could control for ungulate identity (i.e. intrinsic species traits) but not many of the extrinsic mechanisms that drive ecosystem responses to ungulates (e.g. higher stocking densities under more industrialized agriculture, or provisioning of subsidies and extraction of resources; Hempson et al. 2017).

4. Human activities may blur the boundaries between ecosystem effects of wild and domestic ungulates

Finally, research on the extrinsic mechanisms mediating ungulate impacts on ecosystems would benefit from greater consideration of how human activities can transform the ecological effects of wild ungulates as well as domestic livestock. The role of management practices in driving ungulate impacts on vegetation and soils can certainly be taken as an argument in favor of pursuing more sustainable methods of animal husbandry. Yet, the corollary is equally true, but far less frequently discussed. Put simply, under anthropogenic pressures, even native wild ungulates could end up replicating the ecosystem impacts of domestic livestock. Wild ungulate populations are frequently subject to human management, albeit not as directly as domestic species. For example, wild herbivores are hunted for food or culled to reduce competition with domestic stock, impacting population trajectories as well as behavior and movement in anthropogenic landscapes of fear (Abraham et al. 2021, 2023b). In other cases, wild populations in some regions are provided with supplemental food or water to meet conservation and recreation goals (Cotterill et al. 2018). Perhaps most notably, land use change and habitat fragmentation are reducing both overall habitat availability and habitat connectivity for wildlife across the globe (Tucker et al. 2018). In addition to reducing wild ungulate populations overall, this constraining of movement can concentrate wild ungulates in smaller areas, effectively increasing stocking densities in fragmented natural areas (Veldhuis et al., 2019; Western & Mose, 2023). Thus, wild ungulate populations may reproduce many impacts of high-intensity livestock production if human activity leads shrinking natural areas to function similarly to restricted pastures (Table 1).

5. Conclusions

Our review and synthesis of the literature shows that surprisingly little research has directly compared the impacts of wild and domestic ungulate species on plants and soil, and fewer studies still have systematically assessed the mechanisms underlying the (dis)similarity between wild and domestic ungulates' functional roles in ecosystems. Nevertheless, understanding not only *whether*, but *why* wild and domestic ungulates can function similarly in the ecosystems they inhabit is essential to address some of the most pressing questions in agriculture, food security, and environmental protection that communities currently face, and particularly to understand whether domestic ungulates can be managed to reproduce the ecological functions of wild species. Conversely, policies that aim to restore wild ungulate populations under the assumption that their intrinsic traits will promote ecosystem health may fail to account for key extrinsic mechanisms mediating their environmental impacts. Accordingly, further study of the traits and mechanisms that influence the interactions and feedbacks between ungulates, plants, and soils is essential for our ecological understanding as well as the effective management of wild and domestic herbivores alike in the face of global change.

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Supplementary Material:

Table S1