Resolving Indirect Effects of Large Herbivores on Terrestrial Ecosystem Functioning

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Abstract: The world's large herbivores play outsized roles in shaping ecosystem processes like primary production, decomposition, and mineralization. Contemporary management of these animals is therefore poised to be a powerful tool for holistic ecosystem management. Yet we currently lack (i) adequate understanding of indirect interactions underlying herbivore control of ecosystem processes, especially belowground, and consequently (ii) an ability to predict how ecosystems will respond to ongoing changes to large herbivore populations such as (re)introductions, range shifts, and population collapse. In this contribution, we synthesize current approaches to meet these challenges and provide a framework to better resolve indirect effects of large herbivores on terrestrial ecosystem functioning. Specifically, we synthesize empirical evidence from across the globe and demonstrate that the consumptive and non-consumptive effects of large herbivores frequently disrupt and restructure the primary biotic and abiotic controls on ecosystem functioning. Next, we derive an analytical framework and illustrate how empiricists can use this framework to resolve key relationships among large herbivores, biotic/abiotic controls, ecosystem processes, and environmental context. Our framework can uncover emergent patterns that are not revealed with existing approaches. We conclude with a roadmap to operationalizing our framework using existing research infrastructure (e.g., large exclosures and distributed networks).

Key Words: zoogeochemistry, herbivory, megafauna, soil, indirect effects, aboveground-belowground linkages, ecosystem functioning, networks, exclosures

Introduction

Twenty thousand years ago, human beings were in the midst of a global hunt for large herbivores that would transform terrestrial ecosystems for millennia (Svenning et al., 2024). Ecologists have since demonstrated that the world's remaining large herbivores (defined as >2 kg and referred to as "herbivores" throughout, unless otherwise stated; Pringle et al., 2023) continue to play outsized roles in shaping ecosystem processes like primary production, decomposition, and mineralization (i.e., herbivore–ecosystem interactions; Pastor et al., 1998; Ruess et al., 1998; see Appendix S1 for glossary of terms). The loss or gain of these animals, including large wild ungulates, marsupials, reptiles, rodents, and birds, has profound effects on ecosystems (Côté et al., 2014; Schmitz et al., 2014). Wildlife management is therefore poised to be a powerful tool for holistic management of ecosystem functioning (Kristensen et al., 2022; Malhi et al., 2022; Schmitz et al., 2023). Yet, this has not been achieved. Herbivore-ecosystem interactions, though sometimes profound, remain extremely challenging to predict, hindering widespread adoption in ecosystem management decision frameworks (Harrison & Bardgett, 2008; Hyvarinen et al., 2021). This is particularly true of indirect effects belowground, where large herbivores continue to surprise us wherever they go (Sitters & Andriuzzi, 2019; Tomita et al., 2025).

Twenty years ago, ecological theory on aboveground-belowground linkages brought indirect effects of aboveground herbivores on belowground communities and processes (e.g., organic matter turnover) into much clearer view (Bardgett & Wardle, 2003; Wardle et al., 2004). Building on case studies of wild ungulates in savanna (Augustine & McNaughton, 1998;

McNaughton, 1985; Ritchie et al., 1998), boreal (Pastor et al., 1993), and tundra (Olofsson et al., 2001; Pastor et al., 2006) ecosystems, these and other works also proposed correlated variation in plant traits, primary productivity, and soil fertility as the central axes over which the outcome of herbivore-ecosystem interactions varies (Bardgett & Wardle, 2003; Pastor et al., 2006; Wardle et al., 2004). Empirical support for these frameworks, however, is inconsistent or conflicting (Sitters & Andriuzzi, 2019). Yet, the central message has stuck: to progress we must (1) resolve herbivore indirect effects with links to ecosystem functioning, especially belowground (Hunter et al., 2012; Malhi et al., 2022; Monk et al., 2024; Pringle et al., 2023), and (2) describe how environmental context mediates these interactions (Meyer & Leroux, 2023; Sitters & Andriuzzi, 2019; Tuomi et al., 2021).

We synthesize current approaches to meet these challenges and provide a framework to better resolve indirect effects of large herbivores on terrestrial ecosystem functioning. Specifically, we (1) review key concepts and approaches underlying detection of indirect effects of large herbivores in terrestrial ecosystems. We further (2) synthesize evidence that large herbivores modify relationships among diverse properties of ecosystems, especially controls on soil biogeochemistry (Table 1), but find this type of indirect effect has not been adequately incorporated into theory. Thus, we (3) propose a framework to quantitatively resolve these and other indirect effects on terrestrial ecosystem functioning in greater detail. Finally, (4) we discuss operation of the framework to predict herbivore-ecosystem interactions over landscapes, and priorities for future studies.

1. Large Herbivore Indirect Effects in Ecosystem Interaction Networks

The purpose of resolving herbivore-ecosystem interactions is to identify feedbacks that structure ecosystems (e.g., Loreau, 1995; Pastor et al., 1998; Pichon et al., 2024; Sitters & Olde Venterink, 2015; Veldhuis et al., 2014; Wardle et al., 2004). In practice, many researchers do so by developing empirical study-specific conceptual models of hypothesized herbivore direct and indirect interactions in ecosystems (e.g., Andreoni et al., 2024; Andriuzzi & Wall, 2018; Hobbs, 2006; Hunter et al., 2021; Koltz et al., 2022; Liu et al., 2018; Meyer et al., 2025; Piñeiro et al., 2010; Ritchie et al., 1998; Vandegehuchte et al., 2017; Veen et al., 2010). These models, termed ecosystem interaction networks (EIN) (*sensu* Thrush et al., 2021), track hypothesized positive or negative interactions among biotic, abiotic, and ecosystem process nodes (Fig. 1a). Similar to species interaction networks (*sensu* Wootton, 1993), EIN models are agnostic to the specific mechanism of interaction (e.g., trophic, engineering, structural). Rather, emphasis is placed on the strength and direction of interactions. EINs differ from species interaction networks in two main ways. First, EINs explicitly track interactions among biotic nodes (e.g., feeding, competition), between biotic and abiotic nodes (e.g., ecosystem engineering, habitat formation), and among abiotic nodes (e.g., soil structural-chemical relationships), whereas most species interaction networks exclusively track biotic-biotic interactions (but see Legagneux et al., 2012). Second, given the interest in understanding large herbivore impacts on ecosystem processes, EINs often contain interactions between abiotic/biotic nodes and ecosystem processes (e.g., edaphic or decomposer control of nutrient turnover) (e.g., Chen et al., 2013; Roy & Bagchi, 2022) (Fig. 1a). A direct effect is then an interaction between two nodes that occurs independently of any intermediary nodes. An indirect effect is an interaction between two nodes involving at least one intermediary node (Wootton, 2002).

These conceptual models guide empirical data collection and, increasingly, are formalized as statistical tests of the hypothesized causal structure, often using structural equation models to evaluate support for direct and indirect interactions among variables (Eisenhauer et al., 2015; Grace et al., 2010). Many herbivore-ecosystem interaction models reflect a hypothesized interaction chain structure where direct effects on plants and soil environmental properties cascade to soil biota, and ultimately to ecosystem processes such as decomposition (Tuo et al., 2024), net primary production (Chen et al., 2013), nitrogen mineralization (Chen et al., 2013; Meyer et al., 2025; Ramirez et al., 2021), or soil organic carbon formation (Lovell et al., 2025; Wei et al., 2023) (Fig. 1b).

Growing evidence supports herbivore effects on ecosystem functioning via effects on soil organic matter in an interaction chain structure (Fig. 1a). For example, large herbivores directly influence the quantity and stoichiometry of organic inputs to soil via selective consumption of vegetation and subsequent deposition of carcasses and waste products (dung, urine, parturition fluids) (Augustine & McNaughton, 1998; Bardgett & Wardle, 2010; Bump et al., 2009; Ferraro et al., 2023; Hobbs, 1996; Subalusky et al., 2015). Changes to litter quality and quantity may then cascade through soil food webs to impact soil biogeochemistry and ultimately feedback to plants and aboveground fauna (Bardgett & Wardle, 2003; Ferraro et al., 2024; Hunter et al., 2012; Rizzuto et al., 2024; Tuo et al., 2024). Yet, research in soil science and biogeochemistry demonstrates how drivers of soil biogeochemical processes may be multivariate and may not necessarily follow a chain of interactions (Bradford et al., 2016, 2021; Cleveland et al., 2022; Crowther et al., 2019; Ettema & Wardle, 2002; Grandy et al., 2016; Kaspari & Powers, 2016; Prescott, 2010). For example, while organic matter turnover (e.g., decomposition, mineralization) is fundamentally proportional to the quantity of organic substrate (Manzoni & Porporato, 2009;

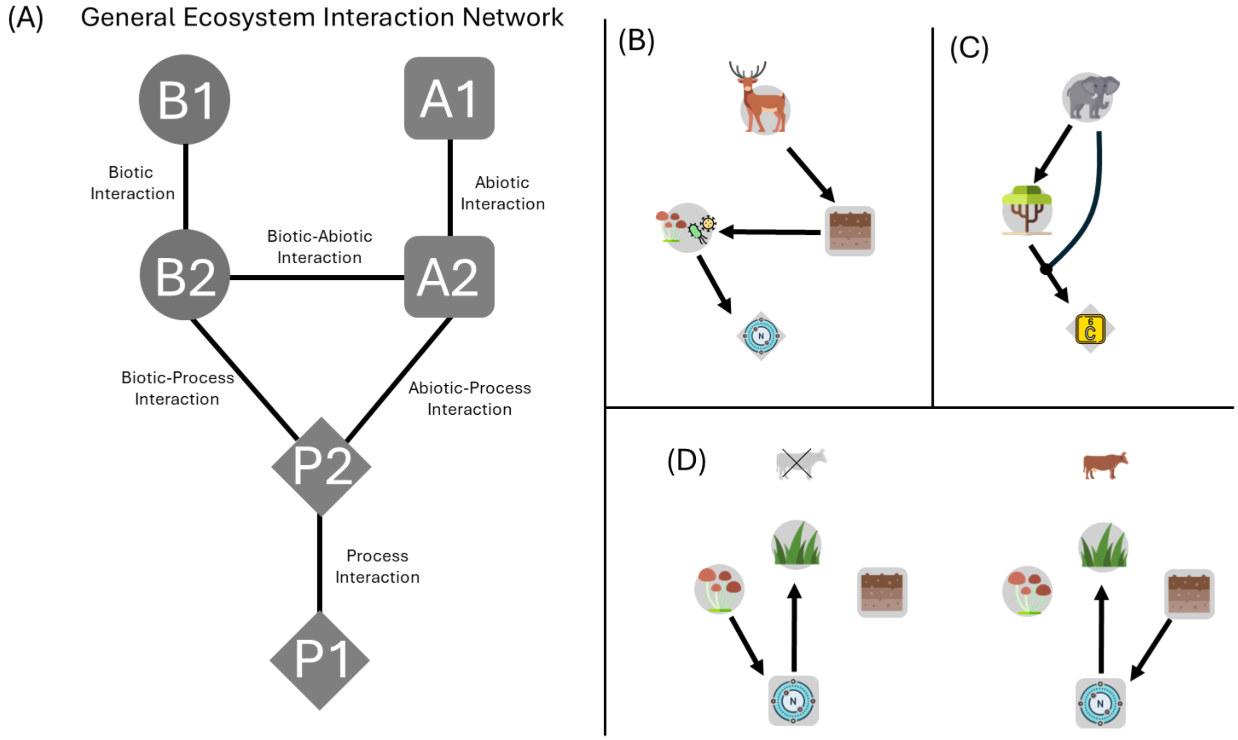

Figure 1. (A) A general ecosystem interaction network (EIN), in which there are six types of interactions among nodes. Given the possibility of feedbacks, cause may occur in any direction depending on the study. In practice, researchers develop a study-specific network to conceptualize hypothesized animal-ecosystem interactions, often as directed acyclic graphs (B-D). (B) Often, researchers test for indirect effects of large herbivores via interaction chain. For example, studies have investigated deer indirect effects on soil nitrogen mineralization via impacts on soil substrate and microbial abundance (e.g., Ramirez et al., 2021; Meyer et al., 2025). (C) Large herbivores can also modify interactions in ecosystems, in parallel with chain effects. For example, elephants reduce the ratio of aboveground to belowground carbon by reducing canopy cover (chain effect) while also strengthening canopy control of AG:BG-C (modification effect) (Kindermann et al., 2025). (D) Interaction modifications can also be detected independently of interaction chains, where large herbivores are considered an external forcing on EIN architecture (Thrush et al., 2021; Zhao et al., 2023). For example, livestock grazers cause a shift from soil chemical (pH) to fungal diversity control of soil-N in temperate grassland (L. Wang et al., 2020).

Swift et al., 1979), turnover rates are also jointly constrained by (micro)climate (e.g., soil temperature), litter stoichiometry (e.g., C:N), soil chemistry (e.g., pH), and decomposer properties (e.g., composition and activity) (Booth et al., 2005; Bradford et al., 2016; Buchkowski et al., 2017; Prescott, 2010). Critically, the relative influence of these controls shifts in space and time according to environmental gradients and thresholds that are still being resolved (Bradford et al., 2016; Prescott, 2010; Bradford et al., 2021).

Herbivore inputs to, and effects on, soil organic matter are clearly important to aboveground-belowground feedbacks (Hunter et al., 2012; Ferraro et al., 2024; Rizzuto et al., 2024; Tuo et al., 2024). Yet, simultaneous interactions with soil microclimate, chemistry, decomposers, and soil fauna remain poorly understood (Sitters and Andruzzi, 2019; Tomita et al., 2025), in part because relatively little research has focused on non-consumptive and engineering effects of herbivores in terrestrial ecosystems (Meyer & Leroux, 2024; Sitters & Andriuzzi, 2019; Tomita et al., 2025; Tuomi et al., 2021). Given the multivariate nature of controls on soil processes (Bernhardt et al., 2017; Prescott, 2010), these pathways must be resolved in greater detail (Sitters and Andriuzzi, 2019). However, in addition to chain effects, large herbivores may act as factors modifying relationships among variables in ecosystem interaction networks, such as controls on ecosystem processes (Fig. 1c,d). This type of indirect effect, called an interaction modification (*sensu* Didham et al., 2007; Foster et al., 2016; Wootton, 1993), is fundamentally distinct from interaction chains. The difference underlies how one conceptualizes herbivore-ecosystem interactions (Fig. 1b,c,d), and therefore matters for managing communities and ecosystems (Didham et al., 2007; Foster et al., 2016), for designing future empirical studies (Wootton, 1993), and for theoretical development in community and ecosystem ecology (Zou et al., 2024). For example, *chains* suggest different animal activities (e.g., trophic and engineering effects) may have additive or opposing effects via different pathways within ecosystem interaction networks (Bardgett & Wardle, 2010; Barthelemy et al., 2019; Hunter et al., 2012; Richards et al., 2025). *Modifications*, however, represent a fundamental shift in network relationships, such as which factors control ecosystem processes at the spatiotemporal scale of herbivory (Fig. 1d; Thrush et al., 2021). If modifications exist, herbivore effects on ecosystem functioning will be difficult to anticipate, scale, or even detect under existing frameworks (Wootton, 2002; Foster et al., 2016).

Appreciation for the distinct role of interaction modifications in the context of food webs (Kéfi et al., 2012; Sanders et al., 2014; Terry et al., 2017), wildfires (Foster et al., 2016), and invasion biology (Didham et al., 2007) is growing. Yet, theory and evidence on the respective role of interaction chain and modification effects underlying herbivore-ecosystem interactions has not been developed (Malhi et al., 2022; Pringle et al., 2023; Trepel et al., 2024; Tuo et al., 2024). In the proceeding sections, we synthesize the breadth of evidence of interaction modification by large herbivores in ecosystems and clarify the distinctions and potential consequences of herbivore effects via interaction chain and modification effects.

2. Evidence of Interaction Modification by Large Herbivores

Across systems, we find large herbivores modify the existence, strength, and functional form of interactions among diverse ecosystem properties and processes (Table 1). We review the breadth of evidence, including modification of spatial and temporal controls on soil biogeochemistry (e.g., soil organic matter dynamics, nutrient availability, carbon storage), and interactions among biotic and abiotic properties of ecosystems.

Modification of spatial controls on soil biogeochemistry

Modification of controls on soil processes, such as soil organic matter (SOM) dynamics, may be particularly important to herbivore-ecosystem feedbacks in terrestrial ecosystems. The primary controls on SOM dynamics are thought to be climate, substrate chemistry, and decomposer properties, which vary heterogeneously across spatial extents (Ettema & Wardle, 2002; Prescott, 2010; Bradford et al., 2016; Manzoni & Poroprato, 2009; Tuo et al., 2024). We find large herbivores modify the nature of all three major controls in ways both striking and subtle. For example, livestock grazers invert a trend of mean annual temperature (MAT) control of decomposition across global drylands (Maestre et al., 2022). Here, temperature control is weakly positive under low herbivore densities, but flips to strongly negative under high densities, over the same temperature range (Maestre et al., 2022). More subtly, large herbivores can modify the extent of soil substrate or microbial control of soil processes. For example, soil nitrogen content controls interannual soil carbon flux in the presence but not the exclusion of ungulates from a Trans-Himalayan montane grassland (Naidu et al., 2022). Similarly, SOM and microbial properties are coupled with summer nitrogen mineralization rates on, but not adjacent to, moose trails in boreal forest (Meyer et al., 2025). Notably, the opposite trend occurs in Chinese temperate grassland, where microbial links to nitrogen and carbon mineralization are stronger in areas of ungulate exclusion than in areas open to large herbivores (B. Wang et al., 2020).

Ecosystem processes and their controls are commonly spatially structured along environmental gradients such as latitudinal climate (Ren et al., 2025), regional topography (Risch et al., 2007; Sitters et al., 2017), geology (Wigley-Coetsee et al., 2022), and long-term ecosystem development (Blaško et al., 2015). Large herbivores can also modify these interactions. For example, the presence of elk in Yellowstone National Park (Augustine & Frank, 2001) as well as caribou in Swedish tundra (Sitters et al., 2017) decouples spatial patterning of soil nitrogen from topographic position. Similarly, herbivores can modify rank-order relationships among ecosystem types. For example, bushland ecosystems have higher N mineralization than glade ecosystems in semi-arid Kenyan savannah, but this spatial structuring is absent in the presence of herbivores (Coetsee et al., 2023). Belowground, soil depth typically exerts strong controls on soil biology and biochemistry (D. Liu et al., 2018; Weldmichael et al., 2020), but this vertical structuring of soils can also be modified by large herbivore presence. For example, soil redox potential and decomposer activity is strongly structured by soil depth in the presence but not the absence of ungulate grazers in a European salt marsh (Schrama et al., 2013). Similarly, browsing by moose and hares in Alaska modifies summer fine root depth profiles, with biomass production shifted substantially to shallower soils (Ruess et al., 1998).

Modification of temporal controls on soil biogeochemistry

Large herbivores also modify temporal controls on soil processes. For example, season is a powerful control on soil biogeochemistry in many ecosystems as water dynamics, temperatures, resource pulses, and biotic phenology (e.g., leaf-out, animal migrations) are in dramatic flux. Yet large herbivores are capable of modifying seasonal trends in soil processes. In some cases this represents a modest shift, such as when the annual N_{min} peak is shifted a month earlier due to wild and livestock ungulate presence in Indian montane grasslands (Bagchi et al., 2017). Other cases are dramatic. For example, large herbivores, such as grazers in semi-arid Kenyan savannah, can dramatically increase monthly fluctuation of soil inorganic nitrogen (Augustine & McNaughton, 2006), or even invert seasonal trends in N mineralization, as with cattle presence in European salt marsh (Bakker et al., 2004). By contrast, large herbivore presence can also reduce (stabilize) soil processes, such as interannual soil carbon flux in montane grasslands (Naidu et al., 2022).

Modification of above- and belowground biotic interactions

Beyond modification of direct controls on soil biogeochemistry, large herbivores also modify biotic interactions relevant to ecosystem processes. Belowground, livestock grazers in temperate grasslands can decouple soil nematode and microbial biomasses (B. Wang et al., 2020) and couple variation in microbial and plant groups (Ma et al., 2024). Similarly, relationships among above- and belowground communities of microbes, invertebrates, and plants, are restructured by successive exclusion of large, medium, and small-bodied herbivores in a European montane grassland, with consequences for ecosystem functioning (Risch et al., 2018). Aboveground, large herbivores can modify diverse overstory and understory interactions (Balandier et al., 2022). For example, white-tailed deer presence in temperate forests can decouple relationships between overstory and understory tree size (Sabo et al., 2017), while moose presence in boreal forest can cause a shift from a linear to non-linear relationship between tree diversity and tree height (Muiruri et al., 2015). Ultimately, these diverse patterns suggest that interactions important for feedbacks in above- and belowground systems (e.g., energy channels; diversity-functioning relationships) can be fundamentally modified by large herbivores.

Modification of soil abiotic interactions

Beyond biotic interactions, large herbivores can also modify relationships among soil abiotic conditions. For example, elk exclusion from coastal California grasslands decouples soil texture from soil moisture and bulk density, which are typically strongly correlated (Dong & Ochsner, 2018). Despite considerable research on ecosystem engineering (biotic-abiotic interactions), herbivore-driven modification of relationships among abiotic conditions in ecosystems has received very little attention (Gutiérrez & Jones, 2006). Yet, core assumptions, like relationships between soil texture and soil hydrology, underly our ability project current field conditions over landscapes (Celik et al., 2022) and the potential response of soil systems to environmental change.

Table 1. Breadth of abiotic-biotic and process interaction modifications by large herbivores.

Modified Interaction	Ecosystem Type	Nature of modification	Reference
Climate control of decomposition and soil-C storage	Global drylands	Livestock grazers inverse a trend of mean annual temperature (MAT) control of decomposition and soil-C storage across global drylands. In both cases, temperature control is weakly positive under low herbivore densities, but flips to strongly negative under high densities, over the same temperature range.	Maestre et al., 2022
Soil-N control of soil-C flux	Montane grassland	Increased soil nitrogen decreases interannual soil-C flux in the presence but not the absence of native (e.g., ibex, bharal, yak) and livestock ungulates in a montane grassland.	Naidu et al., 2022;
Soil moisture control of soil microbial biomass and C_{min}	Montane grassland	Grazing by native ungulates (e.g., ibex, bharal, yak) and livestock ungulates in a Trans-Himalayan grassland decouples variation in soil moisture from variation in soil microbial respiration.	Bagchi et al., 2017
	Tundra	Caribou faecal inputs increase the magnitude soil microbial biomass response to soil moisture in high-arctic tundra.	Van Der Wal et al., 2004
Substrate and microbial control of N_{min}	Boreal forest	Soil organic matter and microbial properties are coupled with summer nitrogen mineralization rates on but not adjacent to moose trails in Canadian boreal forest.	Meyer et al., 2025
	Temperate grassland	In Chinese temperate grassland microbial links to nitrogen and carbon mineralization are stronger in areas of ungulate exclusion than in areas open to large herbivores.	B. Wang et al., 2020
	Saltmarsh	Geese and hare presence weakens soil-N control of N mineralization in European saltmarsh.	van Wijnen et al., 1999
Vegetation and microbial control of soil-N	Tropical forest	Presence of peccaries, tapirs, deer, and other large herbivores/frugivores in tropical forest decouples soil-N availability from N mineralization and facilitates palm control of nitrification rates in amazonian tropical forest.	Villar et al., 2021
	Temperate grassland	Grazing decouples fungal diversity control of soil-N in Chinese temperate grassland (Fig. 1D).	L. Wang et al., 2020
Topographic control of soil N availability	Temperate grassland	The presence of elk in Yellowstone National Park decouples spatial patterning of soil nitrogen from topographic position.	Augustine & Frank, 2001
	Tundra	The presence caribou in Swedish tundra decouples spatial patterning of soil nitrogen from topographic position.	Sitters et al., 2017
Seasonal control of N and C turnover.	Saltmarsh	Cattle presence inverses seasonal trends in N_{min} in European salt marsh.	Bakker et al., 2004;
	Semi-arid savannah	Grazers in semi-arid Kenyan savannah dramatically increase seasonal fluctuations of inorganic soil nitrogen.	Augustine & McNaughton, 2006
	Montane grassland	Presence of wild and livestock ungulates stabilizes interannual trends in soil carbon flux in montane grasslands.	Naidu et al., 2022
Climate control of vegetation biomass and growth	Temperate grassland	Livestock grazers in Chinese temperate grassland shift linear mean annual precipitation (MAP) control of aboveground biomass to a non-linear (hump-shaped) relationship, and decouple MAP control of aboveground litter mass.	Bai et al., 2012
	Boreal/temperate forest and moorland	Pine growth in Scottish highland forest and moorland is more sensitive to MAT in the presence vs. the absence of red deer, roe deer, and other herbivores.	Vuorinen et al., 2020
	Boreal forest	Temperature control of conifer and broad-leafed tree growth is modified by moose in Norway and Canada. Tree growth became more and less sensitive to temperature under moose browsing, depending on tree species and region.	Vuorinen, Kolstad, et al., 2020
	Desert grassland	Large and small herbivores dampen wet season precipitation control of perennial grass cover in a Chihuahuan Desert grassland.	Andreoni et al., 2024
Overstory control of AG-C:BG-C	Semi-arid savannah	Canopy control of the ratio of aboveground to belowground carbon is strengthened by increased elephant density in semi-arid African savannah. (Fig. 1C)	Kindermann et al., 2025
Primary production control of plant diversity	Temperate grassland	Presence of grazers modifies the shape of a non-linear (hump-shaped) relationship between primary production and plant diversity in Yellowstone National Park, USA.	Frank, 2005

Light control of secondary metabolite production	Boreal forest	Moose density in Swedish boreal forest modifies the slope of a positive linear relationships between light and the production of diverse secondary metabolites by bilberry leaves.	Persson et al., 2012
Seasonal control of plant nutrient stocks	Shortgrass prairie	Presence of large, small, domestic, and native herbivores differently modifies seasonal trends in plant stoichiometry including nitrogen, phosphorous, sodium, and silicon content.	Rebh & Welti, 2025
	Tundra	Presence of muskox in the Greenland high arctic modifies seasonal trends in moss aboveground nitrogen pool.	Mosbacher et al., 2019

All of these examples suggest that interaction networks that structure ecosystems are frequently altered by large herbivores. This presents a significant challenge for predicting ecosystem functioning because it suggests that spaces with differing histories, communities, and local intensities of herbivory may functionally diverge as ecosystems develop, and/or respond differently to novel external forcings such as wildfire, drought, warming, or fertilization (Foster et al., 2016). This is clearly true over geological time, over which loss of large herbivores precipitated a continental shift from steppe to forest ecosystems in the global north (Svenning et al., 2024). This process is ongoing in European and North American temperate forests, where long-term forest succession trajectories diverge depending on large herbivore populations (Hidding et al., 2013; Noonan et al., 2021). Yet, even over years and decades, the response of ecosystems to warming (Stark et al., 2023; Väisänen et al., 2014), fertilization (Stark et al., 2023; Veen et al., 2024; Zaret et al., 2023; Zhao et al., 2023), or species introductions (Junod et al., 2025) are meaningfully altered by differences in herbivore density.

Our synthesis reveals the breadth of evidence, and the implication: large herbivore indirect effects do not only propagate through established matter and energy channels; they can rearrange the relevant controls on ecosystem processes. At present, interaction modifications are not measured frequently enough or with enough theoretical consistency to identify general patterns across or even within systems. As researchers continue to resolve sources of heterogeneity in herbivore-ecosystem interactions, we contend that interaction modifications must play a larger part in future studies. In the next section we propose a framework to advance the depth of understanding of herbivore indirect effects on terrestrial ecosystem functioning. Specifically, we identify four key relationships that should be resolved in future studies.

3. A framework to resolve interaction chain and modification effects of large herbivores on ecosystem functioning

We present an analytical framework for resolving all or parts of herbivore interaction chain and modification effects on ecosystem functioning, especially soil processes. Specifically, we connect network, graphical, and mathematical representations of interaction chain and modification effects. In doing so, we highlight key variables, functional relationships, and sources of heterogeneity that should be resolved in future studies. The framework is general and thus applicable across existing fenced, observational, or other field study designs, as well as future meta-analyses or other syntheses of herbivore-ecosystem interactions.

Interaction Chain vs Modification Effects

Nested within any study of indirect herbivore-ecosystem interactions is system-specific evidence, or simply a hypothesis, of what factors directly control ecosystem processes, and how herbivores interact with these variables. Hypothesized interactions are often drawn as a directed acyclic graph (DAG), which then informs field data collection and analysis via structural equation models (SEMs) or other statistical methods.

In the simplest possible model, a process, Y (e.g., N mineralization or decomposition), is related to an abiotic or biotic control, X, according to a relationship $Y=f(X)$. Large herbivore effects on the process, Y, can then occur via chain (Fig. 2) or modification (Fig. 3) effect on this relationship.

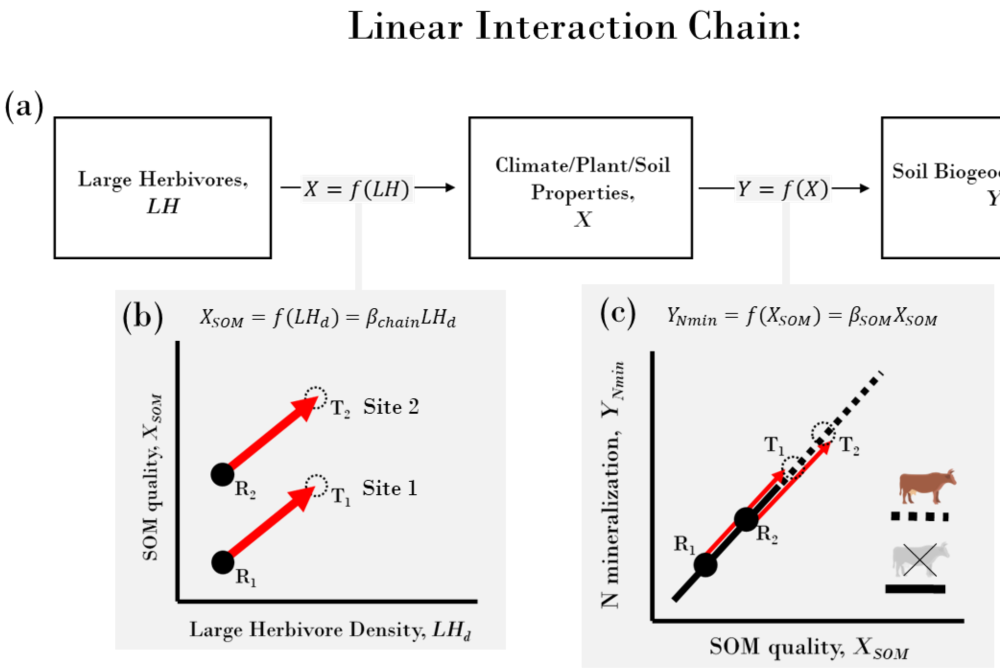

Figure 2. A large herbivore interaction chain in network (directed acyclic graph, DAG), graphical, and statistical form. (A) An ecosystem process, Y, varies as a function of an abiotic or biotic control, X, according to the function $Y=f(X)$. A large herbivore treatment, LH, impacts the process via its relationship to one or more controls, X, according to a function $X=f(LH)$. (B,C) Solid dots and lines represent hypothetical data from Reference (R_i) areas (e.g., no herbivores) including site-specific means (dots) and continuous data (lines). Dashed dots and lines represent data from hypothetical treatment (T_i) areas (e.g., with herbivores). Red arrows track net effects of herbivores through the series of functional relationships. Arrow length is the magnitude of the herbivore net effect. (B) For example, soil organic matter (SOM) quality, X_{SOM}, may vary as a function of large herbivore density, LH_d, according to a function $X_{SOM} = f(LH_d)= \beta_{chain}LH_d$, where β_{chain} is the coefficient of the herbivore effect on X_{SOM}. (C) Herbivore impacts on X_{SOM} then shift N mineralization rate, Y_{Nmin}, according to the function $Y_{Nmin}=f(X_{SOM})= \beta_{SOM}X_{SOM}$.

In an interaction chain, a large herbivore treatment, LH, is causally related to a soil process control, X, via the relationship, $X=f(LH)$ (Fig. 2a). For example, herbivore density, LH_d, may increase soil organic matter (SOM) quality, X_{SOM}, via vegetation consumption and dung deposition (Fig. 2b) (e.g., McNeil & Cushman, 2005). This can in turn increase net nitrogen mineralization, Y_{Nmin}, because mineralization rate is limited by soil organic matter quality throughout the study region according to, for example, a linear relationship, $Y_{Nmin} = f(X_{SOM}) = \beta_{SOM}X_{SOM}$ (Fig. 2c) (Booth et al., 2005; Bardgett & Wardle, 2010). Thus, in an interaction chain, herbivores indirectly increase or decrease values of Y, via their direct effects on values of X, defined by functional relationships among the variables (Fig. 2a). In a well-resolved interaction chain, data from reference and treatment sites occupy different regions of the same relationship between X and Y (Fig. 2c; e.g., Tuomi et al., 2019; Wilson et al., 2018). In a linear interaction chain, the slope of this relationship is the same across reference and treatment sites (Fig. 2c; e.g., Tuomi et al., 2019; Wilson et al., 2018).

In an interaction modification, a large herbivore treatment, LH, is causally related to the coefficient of X (e.g., the slope), β_X, via some relationship, $\beta_X = f(LH)$ (Fig. 3a). For example, temperature, X_{temp} frequently controls decomposition rate, Y_{dec} in ecosystems (Prescott, 2010; von Lützow & Kögel-Knabner, 2009; Xiang et al., 2023). However, large herbivore density, LH_d, may change the coefficient of soil temperature, β_{temp}, via some relationship, $\beta_{temp}=f(LH_d)=\beta_{mod}LH_d$ (Fig. 3b; Maestre et al., 2022). As a result, the relationship between X_{temp} and Y_{dec} is different in treatment vs. reference areas (Fig. 3c). This can occur without a shift in mean soil temperature between reference and treatment areas (e.g., Maestre et al., 2022).

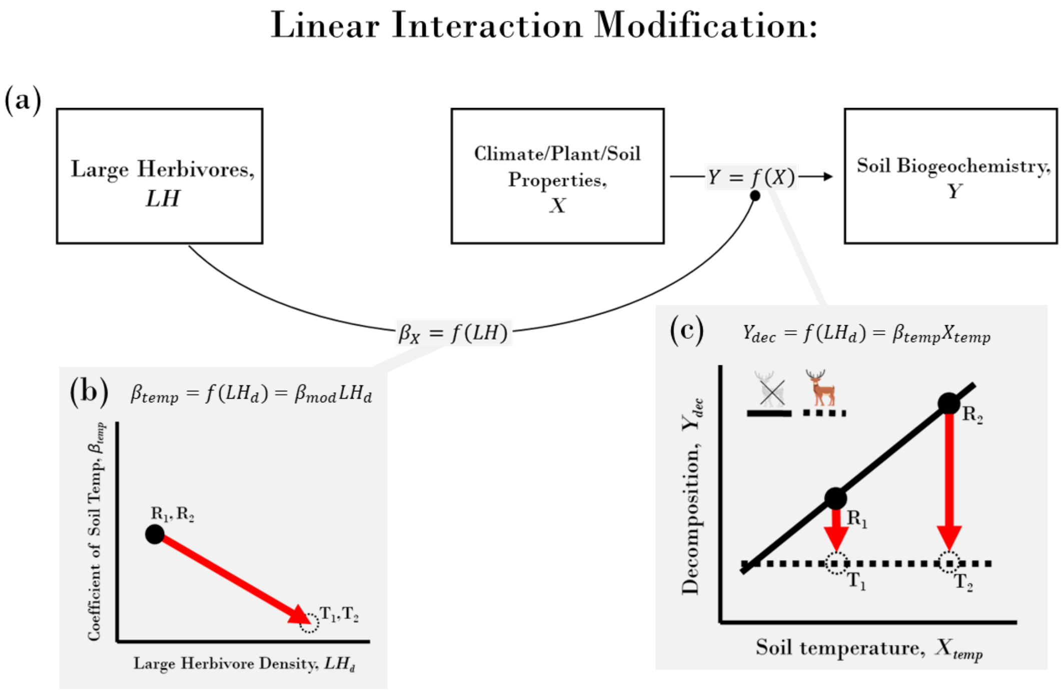

Figure 3. A large herbivore interaction modification in network (DAG), graphical, and statistical form. (A) An ecosystem process, Y, varies as a function of an abiotic or biotic control, X, according to the function $Y=f(X)$. A large herbivore treatment, LH, may then impact ecosystem processes, Y, via its relationship to the coefficient of one or more controls, β_X, according to a function $\beta_X=f(LH)$. (B,C) Solid dots and lines represent hypothetical data from Reference (R_i) areas (e.g., no herbivores) including site-specific means (dots) and continuous data (lines), whereas dashed dots and lines represent data from hypothetical treatment (T_i) areas (e.g., with herbivores). Red arrows track net effects of herbivores through the series of functional relationships. Arrow length is the magnitude of the herbivore net effect. (B) For example, the coefficient of soil temperature, β_{temp}, may vary as a function of large herbivore density, LH_d, according to a function $\beta_{temp} = f(LH_d) = \beta_{mod} LH_d$, where β_{mod} is the coefficient of the herbivore effect on β_{temp}. (C) Herbivore impacts on β_{temp} may then shift temperature control of decomposition, Y_{dec}, according to the function $Y_{dec}=f(X_{temp})=\beta_{temp}X_{temp}$.

Incorporating Higher-Order Environmental Context

We now expand the framework to consider the role of higher-order environmental context (EC) because research frequently demonstrates EC shapes the sign and magnitude of large herbivore effects on ecosystem processes (Bardgett & Wardle, 2003; Ferraro et al., 2023; Forbes et al., 2019; Meyer & Leroux, 2024; Ren et al., 2025; Sitters & Andriuzzi, 2019). Here we define EC as variables (e.g., soil parent material, latitudinal gradients) that are outside the scope of local herbivore effects. We focus on how EC may modify herbivore indirect effects in ecosystem interaction networks (Fig. 4).

In an interaction chain, large herbivores (*LH*) impact abiotic and biotic properties (*X*) via some function, $X=f(LH)$, which in turn shifts soil biogeochemistry (*Y*) according to a function, $Y=f(X)$ (Fig. 2a). In this case, the coefficient of the herbivore effect, β_{chain}, may vary as a function of some higher-order environmental gradient (*EC*) via a relationship, $\beta_{chain} = f(EC)$ (Fig. 4a).

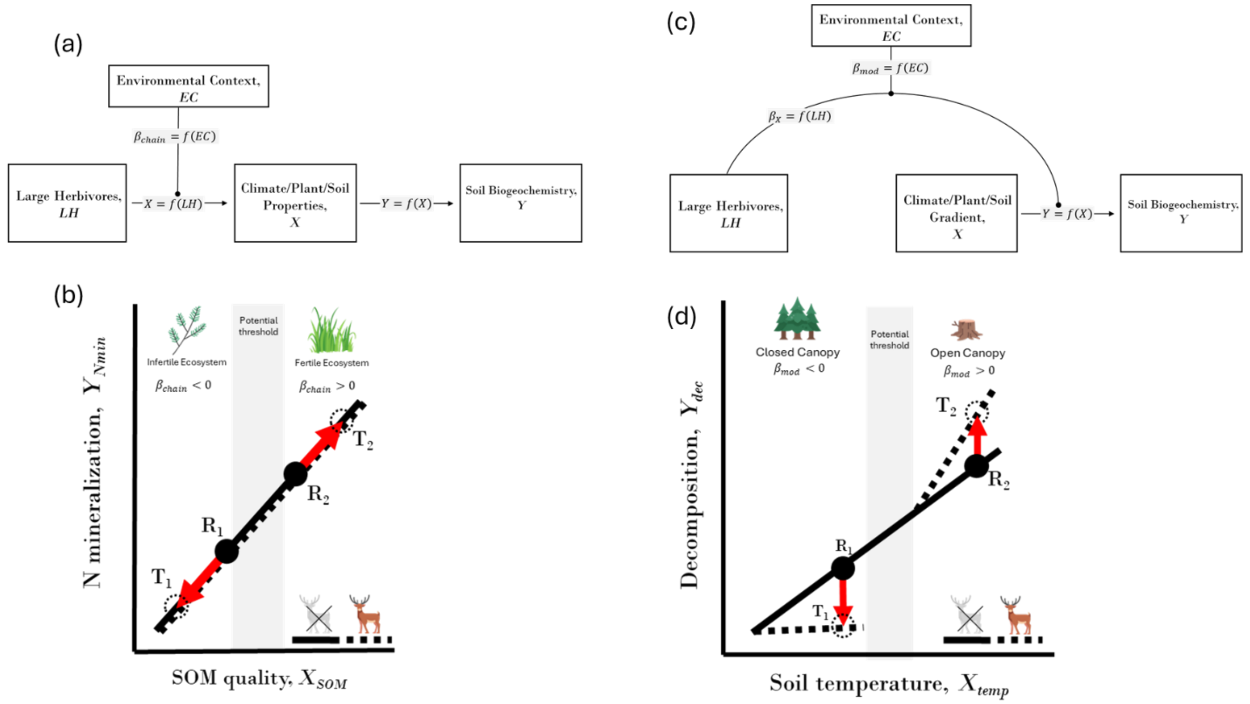

Figure 4. The role of environmental context in large herbivore interaction chain and modification effects on ecosystem processes in network (DAG), graphical, and statistical form. Point and line definitions are consistent with Figs 2 and 3. Variables representing environmental context can modify the coefficients of herbivore chain (A,B) and modification (C,D) effects. (A,B) For example, variation in large-scale ecosystem fertility, EC_{fert}, can modify the large herbivore chain effect on SOM quality, β_{chain}. This creates heterogeneity in the net effect of large herbivores on N mineralization, Y_{Nmin}, (red arrows) despite a consistent relationship between SOM quality and N mineralization, $Y_{Nmin}=f(X_{SOM})= \beta_{SOM}X_{SOM}$, across ecosystems. (C,D) Environmental context can also modify herbivore interaction modifications. For example, where decomposition, Y_{dec}, is limited by soil temperature, X_{temp}, regional variation in forest canopy cover, EC_{cc}, could modify the large herbivore effect on the coefficient of soil temperature, β_{mod}. This creates heterogeneity in the net effect of herbivores on decomposition rates (red arrows) and the local temperature-sensitivity of decomposition, β_{temp}.

The classic model of grazer and browser effects in fast- and slow-cycling ecosystems (Wardle et al., 2004; Pastor et al., 2006) is an example of an interaction chain with herbivore effects modified by environmental context. In these models, large herbivore effects on nutrient cycling occur via their effects on soil organic matter quality, where soil organic matter quality is roughly linearly related to nutrient cycling rates (Bardgett & Wardle, 2003; Wardle et al., 2004; Pastor et al., 2006). However, the direction of the herbivore effect on organic matter quality depends on large-scale climate and plant-based constraints that are independent of large herbivore density, such that large herbivores decrease SOM quality and nutrient cycling in nutrient poor systems, and increase SOM quality and nutrient cycling in nutrient rich systems (Fig. 4b; Bardgett & Wardle, 2003; Pastor et al., 2006). Thus, this model is an interaction chain based on the consistent relationship between organic matter quality and nutrient cycling (Fig. 4b). 'Context-dependent' effects on nutrient cycling occur, because the sign of the coefficient of the large herbivore effect on organic matter quality is related to a large-scale gradient of co-varying climate, plant traits, and soil fertility (Fig. 4b; Wardle et al., 2004). A second example of this is with sheep grazing effects on decomposition and nitrogen turnover over a precipitation gradient (Semmartin et al., 2004).

In an interaction modification, where large herbivores modify abiotic or biotic control of an ecosystem process via some relationship, $\beta_X = f(LH)$, environmental context may in turn define the sign and magnitude of the herbivore-driven modification via some relationship, $\beta_{mod} = f(EC)$ (Fig. 3c). To our knowledge, this interaction structure has yet to be tested. Thus, we present a hypothetical but plausible example to illustrate how this interaction structure may present in the field.

Consider a system where microbial-mediated soil processes (e.g., decomposition) are co-limited by substrate properties (e.g., nutrient availability) and microclimate, such as in temperate and boreal forests (Prescott, 2010; Bernhardt et al., 2017). Here, soil nutrients are heterogeneously distributed, while soil microclimate depends strongly on canopy cover. In this case, large herbivore presence (e.g., deer, boar) modifies the coefficient of temperature control of decomposition, β_{temp}, because the primary local herbivore activities are nutrient deposition (e.g., dung, parturition materials) and soil compaction, which have no chain effect on canopy cover and soil temperature (e.g., Ferraro et al., 2023; Meyer et al., 2025). Canopy cover, EC_{can}, may in turn influence the modification coefficient, β_{mod}, according to some relationship, $\beta_{mod} = f(EC_{can})$ (Fig. 4c). For example, at cooler closed-canopy sites, soil compaction may restrict microbial activity via water-logging (Schrama et al., 2013). As a result, decomposition becomes less sensitive to soil temperature variation across sites with compacted soil (i.e., β_{mod} is decreased; Fig. 3c, lower dashed line). By contrast, at warmer open-canopy sites, higher solar radiation prevents water-logging via compaction. As a result, nutrient depositions make microbial activity less nutrient limited, and therefore more responsive to increased soil temperature (Fig. 4c upper dashed line; Bernhardt et al., 2017; Van der Wal et al., 2004). Thus, decomposition remains temperature-controlled across all sites. However, sites without herbivores (R_1 & R_2) have the same sensitivity, while sites with herbivores (T_1 & T_2) have diverging sensitivities because environmental context (canopy cover) modifies the sign of the large herbivore interaction modification (Fig. 4c).

Non-linear relationships among nodes

We have outlined examples of linear interaction chain and modification effects, and sources of between-site heterogeneity in linear large herbivore effects. However, some abiotic and biotic properties exert non-linear control of ecosystem processes, especially over larger spatial extents (Bradford et al., 2016; Y. Liu et al., 2016; Prescott, 2010). There is also evidence that herbivore density exerts non-linear influence on vegetation and soil properties (Chen et al., 2013) and ecosystem processes (Persson et al., 2007; Tuomi et al., 2021). Non-linear relationships in ecosystem interaction networks present another important source of heterogeneity in herbivore net effects (Appendix S2). Future studies should be cognisant of whether hypothesized controls exert linear or non-linear control over the scale of herbivore treatment effects, and whether there is evidence that herbivore direct effects are non-linear, especially threshold or saturating functions with herbivore density (Chen et al., 2013; Foster et al., 2016; Persson et al., 2007; Tuomi et al., 2021). Fortunately, resolving non-linear relationships involves the same techniques as linear relationships (see Perspectives).

Summary

Overall our framework highlights four key functions that should be resolved in future studies. These are:

$Y_{process}=f(X_{controls})$ (abiotic and biotic controls on ecosystem processes) (1)

$X_{controls}=f(LH_{treatment})$ (herbivore chain effects on abiotic and biotic controls) (2)

$\beta_X=f(LH_{treatment})$ (herbivore modification effects on abiotic and biotic controls) (3)

$\beta_{mod/chain}=f(EC)$ (environmental context control of herbivore effects) (4)

Thus, we contend future studies should move beyond describing the net effects of large herbivore treatments on ecosystem processes, and move towards establishing how large herbivores relate to the functions describing direct controls on ecosystem processes at spatiotemporal scales matching the scope of herbivore treatment effects (equation 1). This entails resolution of the functional relationships of *LH* to the value of biotic and abiotic controls (equation 2) and their coefficients (equation 3). This is the core of establishing large herbivore effects on soil biogeochemistry via interaction chains and interaction modifications. Finally, studies should also consider how/whether variability in higher-order environmental context mediates large herbivore effects (equation 4), and the most important variables representing this context. Our framework, therefore, helps organize relationships among key variables, relationships, and sources of heterogeneity in herbivore-ecosystem interactions, which should be resolved in future empirical studies including primary data collection and meta-analyses (see Perspectives). In the next section, we apply our framework to questions in spatial soil ecology, and demonstrate how resolving interaction modification effects of herbivores could improve prediction of large herbivore-ecosystem interactions over landscapes.

4. Perspectives

A major theme of past herbivore-ecosystem interaction research has been identifying the scope of indirect effects of large herbivores above- and belowground (Foster et al., 2014; Tomita et al., 2025; Tuomi et al., 2021; Wardle et al., 2001). Our framework offers a detailed template for resolving indirect effects underpinning large herbivore-ecosystem interactions and the role of environmental context in mediating large herbivore indirect effects. Doing so, however, may require a shift from traditional empirical methods in line with recent perspectives in soil biogeochemistry (Bradford et al., 2021). We discuss this point with a critical look at classic fence-based field studies and a discussion of key unresolved questions in large herbivore-ecosystem interactions.

4.1 Challenges and opportunities for future empirical research

Classic fence designs

The prototypical method of quantifying large herbivore-ecosystem interactions is comparing ecosystem properties on either side of a fence separating treatment and reference areas (Forbes et al., 2019). Often, the treatment limits or removes herbivore access to an area with a fenced exclosure, while an adjacent reference area remains open to herbivores (e.g., Wigley-Coetsee et al., 2022). In other cases the design is reversed; large herbivore densities are controlled in treatment enclosures, with no herbivores in reference areas (e.g., Chen et al., 2013).

In single field studies as well as meta-analyses, fence designs are commonly used to measure a herbivore 'net effect' with mean comparisons of treatment vs. reference areas (e.g., ANOVA, response ratios) (Forbes et al., 2019; Trepel et al., 2024; Tuo et al., 2024; Ren et al., 2025). With this design, interactive effects of a herbivore treatment with other categorical factors, such as ecosystem type, additional experimental treatments (e.g., fertilization), other site factors (e.g., high vs. low vegetation diversity), or simply 'site' itself, are commonly reported in field studies (Bressette et al., 2012; Pastor et al., 1988; Persson et al., 2009; Stark et al., 2003; Zhao et al., 2023). Interactive effects of this nature reveal a causal (if coarse) mechanism for observed patterns, and provide qualitative insight into ecological contingencies. This effect is sometimes called a 'first-order' mechanism because high-level cause is established (e.g., herbivore exclusion) but specific direct and indirect interactions are not (i.e., EIN structure; Figs. 1-4; Pringle et al., 2023).

Using fence designs for prediction

While extremely valuable as a starting point, these results are insufficient to predict herbivore-ecosystem interactions in novel contexts because observed patterns can arise from several potential EIN structures (Fig. 5). For example, a case where herbivores increase a response variable at one site but not another (Fig. 5a), could arise from indirect effects via interaction chain (Fig. 5b) interaction modification (Fig. 5c). These interaction structures return dramatically different predictions of an ecosystem process with respect to variation in controls (Fig. 5b,c solid vs. dotted lines). A second interactive effect, where sites have qualitatively different responses to a herbivore treatment, can also result from a herbivore interaction chain or interaction modification (Fig. 5d-f). Still more interaction structures may produce these patterns if one relaxes the assumption of linear relationships among nodes (Appendix S2). In either case, understanding the nature of herbivore indirect effects may have profound consequences for predicting ecosystem processes over landscapes, including spatial patterning and heterogeneity (Box 1). There is growing evidence that large herbivores indeed alter spatial heterogeneity in soil processes (Ferraro et al., 2022; Murray et al., 2013; Trepel et al., 2024). Whether this patterning suggests soil processes also become less predictable over landscapes under herbivory, or simply represents a reorientation of relevant controls, has not been tested (Box 1). Overall, greater resolution of indirect interaction structures among large herbivores, ecosystem processes, and their abiotic/biotic controls will improve prediction of patterns over landscapes.

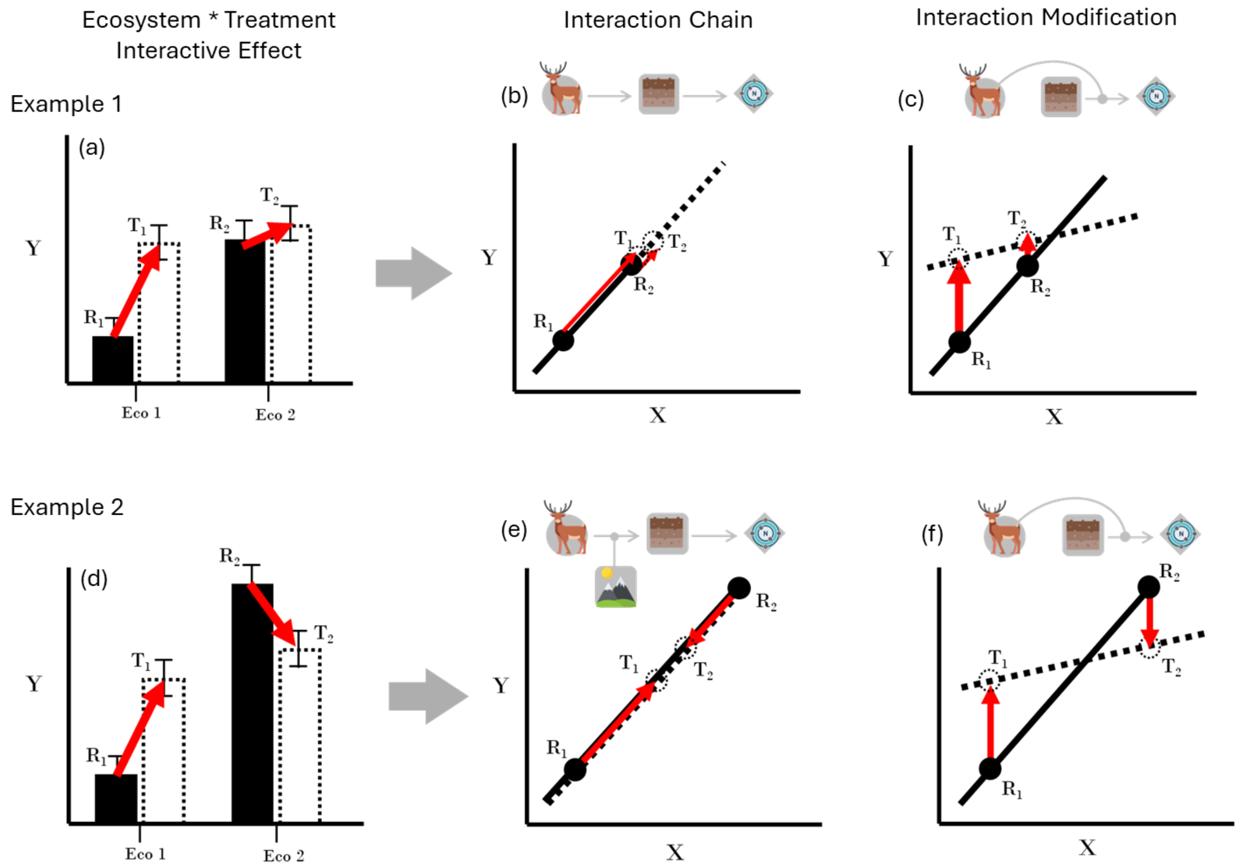

Figure 5. Interactive effects of *Site* (e.g., ecosystem type) and *Treatment* (e.g., herbivore density) factors (A, D) on an ecosystem response, *Y* (e.g., N mineralization) can result from interaction chain (B, E) or modification (C, F) network structures. Line and symbol definitions are consistent with Figs 1-4. (A, D) Results from hypothetical herbivore-ecosystem field studies in which Reference conditions differ between sites. Example 1: (A) Herbivores increase *Y* in Ecosystem 1 but have no significant effect in Ecosystem 2. This pattern can result from, for example, an interaction chain where the magnitude of the herbivore treatment also differs across sites (B), or an interaction modification that decreases the coefficient, β_X, over the full range of *X* (C). Example 2: (D) A hypothetical interactive effect in which herbivores increase *Y* in Ecosystem 1 and decrease *Y* in Ecosystem 2. This pattern can result from, for example, an interaction chain where the coefficient, β_{chain}, depends on higher-order environmental context (EC), or an interaction modification that decreases the coefficient, β_X, over the full range of *X* (F).

Using fence designs to understand contingencies

Designing studies to differentiate herbivore chain or modification effects can also help researchers find causality in site-level contingencies. For example, in a linear chain effect, heterogeneity in the net effect implies that the magnitude of the herbivore treatment (e.g., local density) differs across sites (Fig. 5b). This is common in fenced designs, where herbivore densities cannot be precisely controlled in reference plots adjacent to exclosures, and available density data may not match the scale of measurement. For example, local impacts may be higher or lower than regional densities suggest. Alternatively, site-level chain effects may differ because of site variation in higher-order environmental context (Fig. 5d,e). This is particularly likely if the sign of the herbivore effect differs between sites (e.g., Fig. 5d,e). By contrast, in a modification effect, the position of each site along the *X* axis itself influences the direction and magnitude of the herbivore net effect on *Y* (Fig. 5c,f). In practice, study sites in exclosure-based designs can be very different (e.g., in plant-soil communities, edaphic properties, microclimates), even in the same region (e.g., Bressette et al., 2012; Ellis & Leroux, 2017; Swain et al., 2023). In either case, resolving the nature of herbivore indirect effects (chain or modification) can leave researchers with clear and testable hypotheses for why contingencies occur, which is essential for building causal understanding over successive studies (Grace, 2024).

Box 1: Modification of spatial soil heterogeneity by large herbivores

The predictability of soil functioning is of primary concern for anyone trying to project current or future patterns of soil biogeochemistry of over landscapes (e.g., Crowther et al., 2019; Ren et al., 2025; Rizzuto et al., 2024; Wilson et al., 2025). Soil factors controlling ecosystem processes are spatially structured (Ettema & Wardle, 2002). For example, substrate quality (e.g., organic matter C:N) and soil chemistry (e.g., pH) are jointly constrained by litter traits, and are frequently correlated across sites (e.g., Högberg et al., 2017). Other factors, such as microclimate and soil organisms, may vary independently over landscapes (Bernhardt et al., 2017; Ettema & Wardle, 2002). Spatial heterogeneity in the distributions of multiple soil properties creates spatial heterogeneity in soil functioning (Bernhardt et al., 2017; Crowther et al., 2019; Nunan et al., 2020; Fig. 6).

Herbivore interaction modifications may have profound consequences for spatial patterning of soil processes (Fig. 6). For example, a myriad of potential effects, such as herbivore impacts on surface albedo, soil structure, or microbial communities, may shift the relative control of soil functioning by substrate (e.g., %N) vs microclimate (e.g., degree days) properties (Fig. 6). Depending on the spatial patterning of substrate and microclimate controls, large herbivores could shift spatial patterning of soil functioning from highly patchy to gradient-based (Fig. 6). Herbivore effects on decomposer community composition (e.g., Aggerbeck et al., 2022; Eldridge et al., 2020) may be a primary mechanism underlying such a modification because distinct functional traits, physiologies, and resource limitations of microbial communities define their roles in soil functioning (Fierer et al., 2007; Hicks et al., 2022; Ribbons et al., 2016; Strickland et al., 2009; Waring et al., 2013).

This simple application illustrates how even small interaction modifications may be quite influential in ecosystems where soil processes are strongly co-limited, such as arctic tundra (temperature and nutrient colimitation) and drylands (water and nutrient co-limitation), compared to warm and wet systems (e.g., tropical forests) where autotrophic and heterotrophic activity are strongly nutrient limited. Of course, these hypotheses need testing. We contend that resolving herbivore modification of spatial soil ecology is an important area for future study that can improve prediction of ecosystem functioning over landscapes.

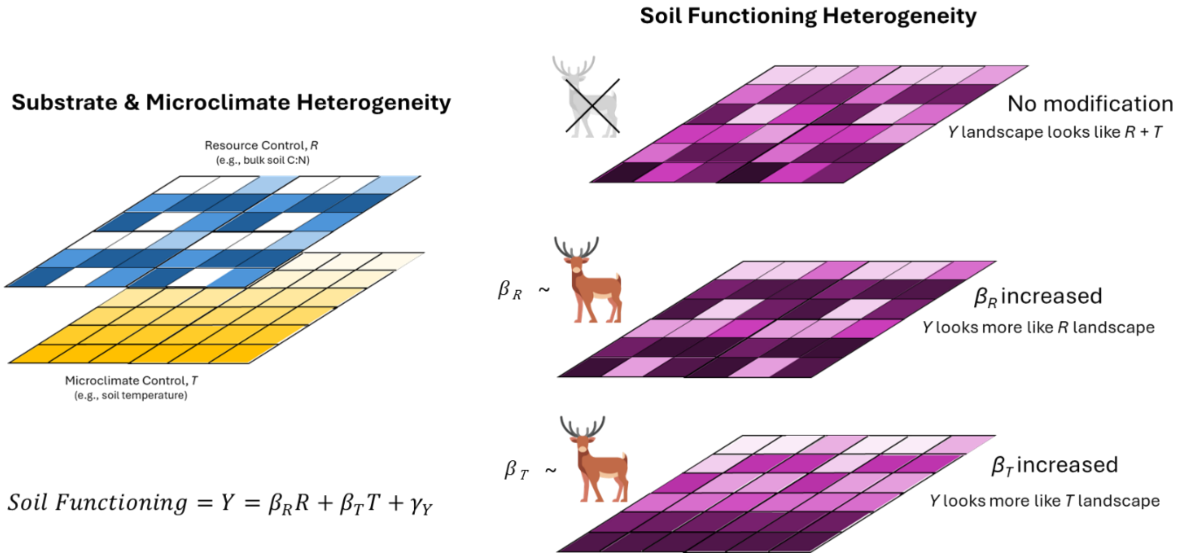

Figure 6. Large herbivores may shape spatial soil patterns via interaction modifications. (A) Variation in soil processes (e.g., decomposition, nutrient cycling) is often explained by variation (cell shade) in multiple independent variables with independent spatial patterning. (B) In absence of large herbivores, spatial patterning of soil functioning reflects the additive effect of joint substrate and microclimate controls. (C) In the case where large herbivores increase the coefficient of substrate control, β_R, soil functioning, Y, more closely reflects landscape patterning of the soil substrate variable (i.e., Y becomes more patchy). (D) In the case where large herbivores increase the coefficient of microclimate control, β_T, soil functioning, Y, more closely reflects landscape patterning of the soil microclimate variable (i.e., a linear gradient in Y emerges).

Operationalizing our framework in future designs

Despite some challenges, fence designs will continue to play an important role in large herbivore research (Pringle et al., 2023). In line with recent perspectives in spatial SOM dynamics (Bradford et al., 2016; Bradford et al., 2021), resolving the equations in our framework likely requires a shift from pooling individual samples physically (e.g., combining soil cores) or statistically (e.g., as means), toward identifying relationships among variables based on continuous data collected at the same resolution (Bradford et al., 2021). This also means establishing experimental or observational gradients over which environmental context, *EC*, and large herbivore treatments, *LH*, can change gradually (Meyer & Leroux, 2023). This is difficult to do in practice, but designs that repeat treatments and sampling across adjacent ecosystem types offer a good start (Kindermann et al., 2025; Meyer et al., 2025). Emerging methods, such as advanced use of camera traps (Carswell et al., 2025) and quantification of herbivore fecal biomarkers in soil (Karp et al., 2025) also provide a path towards establishing herbivore abundance gradients at finer resolutions and with greater accuracy. Ultimately, resolving the functional form of relationships among all important nodes in ecosystem interaction networks is unlikely to be feasible within any single study. Integrating evidence across studies and approaches is therefore critical to building causal understanding (Grace, 2024).

To this end, observational studies, or those pairing observational and experimental designs, circumvent some of these challenges by choosing sites for local treatments (e.g., material deposition, trampling) along gradients in site properties (Ferraro et al., 2023; Meyer & Leroux, 2023; Moran et al., 2025), and over a range of present/historic herbivore treatment intensity (Meyer et al., 2025; Moran et al., 2025; Ren et al., 2025). The obvious downside is a lack of complete experimental control. Here, there is great potential for green-house experiments to resolve the equations we identify at the scale of individual plants and their rhizosphere (e.g., Mikola et al., 2001). At the other end of the spectrum, some exclosures are extremely large (e.g., Wigley-Coetsee et al., 2022) or specifically designed to cross gradients in ecosystem properties (e.g., habitat productivity; Persson et al., 2007), which could help resolve these relationships at larger spatial extents (Pringle et al., 2023; Wigley-Coatsee et al., 2022; Sitters et al., 2017). We feel there are many opportunities for researchers working independently to link existing infrastructure or create new distributed networks aimed at resolving the equations we identify in our framework within and across systems (e.g., Keller et al., 2025; Petersen et al., 2023).

Distributed networks or coordinated sampling protocols may help solve another key source of heterogeneity: study-specific definition of ecosystem interaction networks. Whether an indirect effect appears as an interaction chain or modification depends at times on node definition decisions made by the observer (Box 2). This challenge has also been flagged in species interaction research (Brimacombe et al., 2025; Wootton, 2002) but applies to biotic and abiotic variables in EINs as well (Box 2). The ability to construct ecosystem interaction networks to suit specific questions is a strength of the approach. However, the diversity of networks concocted by independent researchers also makes cross-ecosystem comparison an ongoing challenge (Brimacomb et al., 2025). Ultimately, researchers should be aware of this challenge, particularly for evidence synthesis (Box 2; Brimacomb et al., 2025).

Broader adoption of an EIN approach to large herbivore ecology has the potential to reveal new indirect effects and common interaction motifs across systems, analogous to those found in species-based networks (Olff et al., 2009). For example, the community interaction network model (*sensu* Wootton, 1993) has lead to considerable theoretical development of the nature of indirect effects in ecological communities, including a typology of trait-mediated, density-mediated, and environment-mediated indirect effects (Wootton, 2002), the identification of important network motifs such as alternative forms of omnivory (McLeod & Leroux, 2021), and identification of generalizable network patterns such as predator or resource control of primary production (Oksanen et al., 1981; Ripple et al., 2016; Schmitz, 2008). It is possible that an EIN approach to herbivore-ecosystem interactions will bring about similar generalizations about interactions connecting biotic entities, abiotic properties, and ecosystem processes across systems. For example, interaction chains and modifications stemming from simultaneous engineering and trophic activities of large herbivores may have similar structures in EINs across systems, but such comparisons are not feasible with existing data.

Box 2: The Network Definition Problem

A methodological challenge in disentangling chain and modification effects is that there are cases where the same pattern or process may present as a chain or a modification depending on the observer's definition and measurement of the network (Wootton, 2002). For example, consider an aboveground-belowground system where different microbial groups exert control on elemental cycling via some relationship proportional to their biomass, and a herbivore treatment impacts the relative abundances of microbial decomposers, but not their summed biomass. When microbial biomasses are measured by functional group, a model of indirect effects (e.g., SEM) would find changes in elemental cycling result from multiple simultaneous chain effects, where decomposer biomasses are increased or decreased by a herbivore treatment, while group-specific microbial coefficients with respect to elemental cycling remain fixed (Fig. 7a). By contrast, when total microbial biomass is measured as a single pool, the same change in elemental cycling by herbivores via decomposers would present as an interaction modification, where herbivores modify the coefficient of microbial biomass with respect to elemental cycling (Fig. 7b).

This phenomenon can also apply to abiotic variables. For example, researchers sometimes measure soil organic matter (SOM) based on distinct physiochemical properties that differently influence soil processes (e.g., particulate, mineral-associated, and dissolved organic matter) (von Lützow & Kögel-Knabner, 2009; Xiang et al., 2023). Other times, SOM is measured as a single pool. In the former case, a herbivore-driven change in the proportion of each fraction would present as an interaction chain. In the latter, a change in the relative proportion of different fractions would present as a change in the SOM coefficient with respect to the response variable (e.g., elemental cycling).

Ultimately, any variables that can be easily aggregated or disaggregated based on 'traits' are especially vulnerable to this kind of design-based heterogeneity.

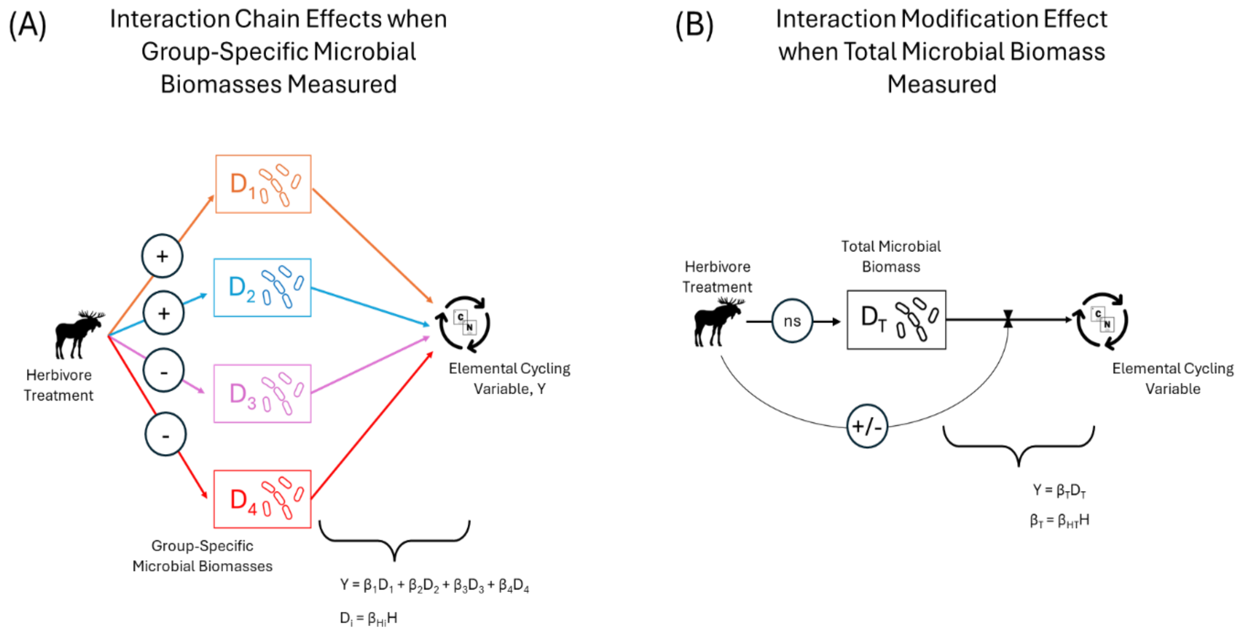

Figure 7. Alternative chain and modification models of the same indirect effect of large herbivores on elemental cycling via decomposers. DAG notation is consistent with Figs 2-4. The circled +, -, and ns, indicate the sign of the herbivore coefficient, β_{LH}, is positive, negative or not significantly different from zero, respectively. In a hypothetical system, microbial groups differently influence elemental cycling via some relationship proportional to their biomass, $\beta_i D_i$. A herbivore treatment, *LH*, then impacts the relative abundance of microbial decomposers, but ultimately not their summed biomass. (A) Multiple simultaneous chain effects emerge when microbial biomass is measured by functional group. Herbivores increase or decrease microbial biomasses while microbial coefficients (β_i) remain fixed. (B) A single interaction modification emerges when microbial biomass is measured as a single pool. Large herbivores modify the coefficient of microbial biomass, β_M, with no chain effect on total microbial biomass, D_T.

4.2 Key knowledge gaps

We have discussed ways our framework can be operationalized in empirical studies. We expand on this discussion with a perspective on the prevalence, scale, and mechanisms underlying herbivore interaction chains and especially modifications in EINs.

Prevalence

Our synthesis suggests herbivore-driven interaction modifications are relatively common and globally distributed (Table 1). Yet, there are also reported cases where biotic-abiotic interactions are not modified by large herbivores (e.g., Frank & Groffman, 1998; Sankaran & Augustine, 2004; Stephan et al., 2017). This is good news! Identifying system interactions that are resilient to large herbivores (and thus constrained by other factors) is critical to understanding and predicting herbivore-ecosystem interactions, but such evidence is currently sparse. This is likely in part because such relationships are less frequently tested, and we have argued that interaction modifications deserve greater attention. Alternatively, there is always the risk of a publishing bias against negative results (Wood, 2020). We therefore encourage researchers and editors to overcome the "file drawer" problem and find a home for these important negative results.

Scale

Large herbivore-driven interaction modifications may emerge more at some scales of organization, space, and time, than others. For example, chain effects of large herbivore consumption and nutrient deposition are highly local in many cases (e.g., Ferraro et al., 2023) but can also appear over larger spatial extents (Ren et al., 2025). Examples from our synthesis range from regional (Meyer et al., 2025) to global (Maestre et al., 2022). Given that for many large herbivores, the proportion of biomass consumed and the quantity of material transported is relatively small compared to total system biomass in terrestrial ecosystems, interaction modifications may represent a primary way in which herbivores effects on vegetation and soil manifest at large spatial extents (Daufresne, 2021).

Mechanisms

Ecological mechanisms exist along a gradient of biological organization (Pringle et al., 2023). Resolving indirect interaction chains and modifications by herbivores in ecosystem interaction networks improves mechanistic understanding of herbivore-ecosystem interactions by moving beyond so called ‘first-order’ mechanisms (Pringle et al., 2023). However, knowing which herbivore activities underly chain and modification patterns is also important, but rarely clear. Ecosystem engineering is a likely mechanism underlying interaction modifications since it amounts to an environmental change impacting many variables simultaneously (Guiterrez & Jones, 2006). For example, moose trampling modifies soil microclimate, substrate, and microbial relationships with N_{min} in boreal forest (Meyer et al., 2025). However, nutrient redistribution can also underly interaction modifications. For example, caribou-vectored nutrient flow (waste deposition) is primarily responsible for modifying topographic patterns of soil fertility in arctic tundra (Sitters et al., 2017). Indeed, nutrient flows by large animals may be a primary mechanism by which topographic structuring of biogeochemistry is modified (Doughty et al., 2016). Thus, interaction modifications result from trophic and non-trophic activities of large herbivores. Following similar approaches to interaction chains (e.g., Chen et al., 2013; Lovell et al., 2025; Meyer et al., 2025), future work must disentangle the extent to which different herbivore activities modify relationships among variables relevant to ecosystem functioning.

Conclusions

From deserts to grasslands, forests to tundra, and marshes to shrublands, we know that large herbivores are at once choosy and voracious eaters, spreaders of seeds, fertilizer and organic matter, earth-movers, and trail blazers. These activities are deeply integrated within ecosystem interaction networks, which are being resolved in greater detail (e.g., Ferraro et al., 2024; Kamaru et al., 2024). The challenge now is to understand the precise nature of these actions in complex interaction networks, and the consequent feedbacks driving stability or change in ecosystems. To this end, we have clarified the nature of indirect effects of large herbivores on soil biogeochemistry via interaction chains and interaction modifications. We have argued that interaction modifications represent an underappreciated yet core feature of herbivore-ecosystem interactions that future research must resolve. We provide a framework to guide this research. We believe that doing so will facilitate a deeper understanding of mechanisms underpinning herbivore-ecosystem interactions to advance sustainable and ethical ecosystem management.

Acknowledgements:

Funding was provided by the Natural Sciences and Engineering Research Council (NSERC) Discovery Grant to Shawn J. Leroux. We thank M. Rizzuto and Y. Wiersma for helpful feedback on earlier drafts of the manuscript.

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Appendices to:

Resolving indirect effects of large herbivores on terrestrial ecosystem functioning

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Supplementary material:

Appendix 1: Glossary of terms

Appendix 2: Non-linear relationships in ecosystem interaction webs

Appendix 1: Glossary of Terms

Abiotic: Describes a non-living feature of an ecosystem (e.g., temperature).

Biotic: Describes a living feature of an ecosystem (e.g., biomass).

Direct effect: An interaction between two variables that occurs independently of other variables.

Ecosystem interaction network: A conceptual or statistical model mapping causal relationships among nodes, where nodes are logical constructs or measurable variables. Nodes include biotic entities or properties (e.g., organism biomasses), abiotic properties (e.g., soil moisture or temperature), and ecosystem processes (e.g., decomposition, mineralization).

Ecosystem process: A material or energy transition from one form to another in time (e.g., soil organic matter turnover, primary production) jointly facilitated by biotic entities and abiotic conditions.

Environmental context: An influential feature of an ecological system with stable dynamics over the spatiotemporal and organizational scale of measurement of a large herbivore variable (e.g., abundance) and its direct and indirect effects in an ecosystem. What is considered contextual therefore depends on the spatiotemporal and organizational scale of consideration.

Herbivore–ecosystem interaction: A causal relationship between some feature of herbivory such as abundance, density, diversity, consumption, or trampling, and an ecosystem process.

Indirect effect: An interaction between two variables that is mediated in some way by at least one additional variable.

Interaction: A causal relationship between two variables.

Interaction chain: An indirect effect in which an initiating variable elicits a change to the values of a series of other variables according to the functional relationships among them.

Interaction modification: An indirect effect in which an initiating variable elicits a change in the functional relationship between two other variables.

Interactive effect: A significant non-additive effect of two independent factors on a response variable in a statistical model, such as a significant multiplication term in an analysis of variance (ANOVA).

Appendix 2: Non-Linear Relationships in Ecosystem Interaction Webs

Our framework highlights four key functions to better organize large herbivore indirect effects on ecosystem processes (equations 1-4). In the main text, we introduce these with linear examples (Figs. 2-5). Non-linear examples are also possible and we explore these in this appendix. Acknowledging the full scope of patterns emerging from relationships among four non-linear functions is infinite, we focus on several notable cases and their implications for resolving inconsistent herbivore effects among study sites, based on existing empirical evidence and recent syntheses.

Case 1: Direct controls on ecosystem processes, $Y_{process}=f(X_{controls})$ (eq.1), are non-linear

Some controls on soil biogeochemistry are non-linear over the spatial scale of measurement (Bradford et al., 2016, 2021; Liu et al., 2016; Prescott, 2010). Alternatively, some properties may exhibit saturating relationships to soil processes, such as temperature control of SOM turnover (Bradford et al., 2016; Bradford et al., 2021).

Interaction Chains

In either this case, the direction and magnitude of a herbivore indirect effects on *Y* via *X* (i.e., an interaction chain) will strongly depend on the positioning of Reference sites along local gradients of *X* (Fig. S1). For example, large herbivore presence can increase soil temperatures via reduced vegetation cover (Kolstad et al., 2018; Meyer et al., 2025; Trepel et al., 2024; Tuomi et al., 2021). However, while SOM turnover is often temperature controlled (Bradford et al., 2021; Colman & Schimel, 2013), herbivore-induced increases in temperatures do not consistently cascade to increase microbe-driven process rates (Kolstad et al., 2018; Meyer et al., 2025; Tuomi et al., 2021). One potential explanation is that temperature control of SOM dynamics is non-linear over the range of herbivore-effected sites, such as the saturating functions described in recent syntheses (Fig. S1; Bradford et al., 2016; Bradford et al., 2021).

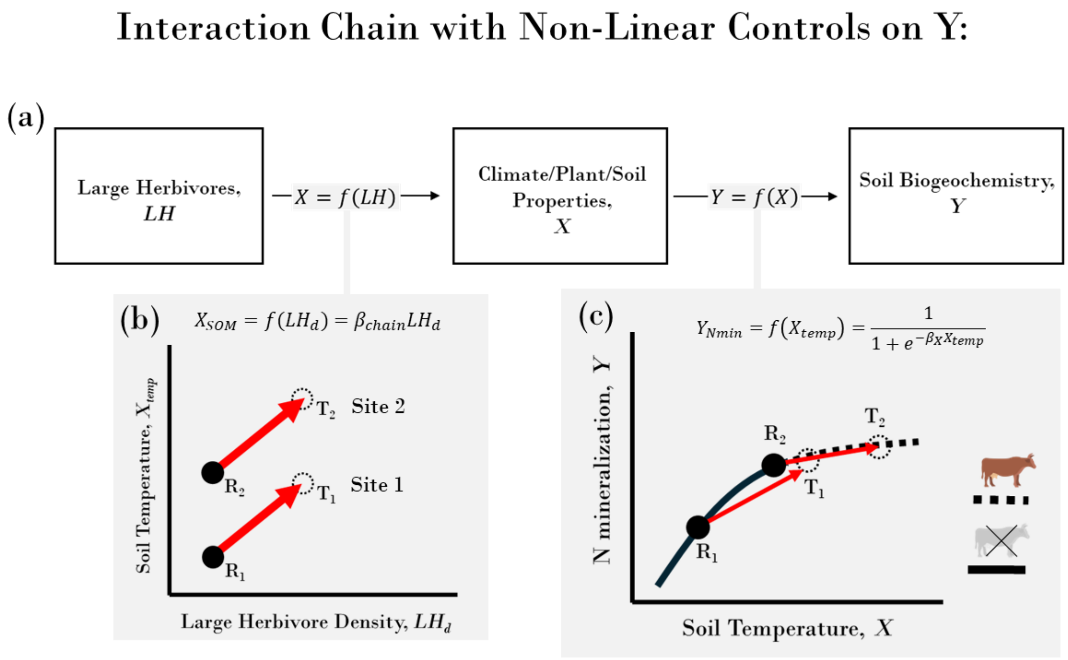

Figure S1. An interaction chain where control of an ecosystem process is nonlinear, represented in network (directed acyclic graph), graphical, and statistical form. (A) An ecosystem process, *Y*, varies as a function of an abiotic or biotic control, *X*, according to the function *Y=f(X)*. A large herbivore treatment, *LH*, impacts the process via its relationship to one or more controls, *X*, according to a function *X=f(LH)*. (B,C) Solid dots and lines represent hypothetical data from Reference (R_i) areas (e.g., no herbivores) including site-specific means (dots) and continuous data (lines). Dashed dots and lines represent data from hypothetical treatment (T_i) areas (e.g., with herbivores). Red arrows track net effects of herbivores through the series of functional relationships. Arrow length is the magnitude of the herbivore net effect. (B) For example, soil temperature, X_{temp}, may vary as a function of large herbivore density, LH_d, according to a function $X_{temp} = f(LH_d) = \beta_{chain} LH_d$, where β_{chain} is the coefficient of the herbivore effect on X_{temp}. (C) Herbivore impacts on X_{temp} then shift N mineralization rate, Y_{Nmin}, according to the function $Y_{Nmin} = f(X_{temp})$.

Interaction Modifications

Modification of non-linear controls of ecosystem processes by large herbivores is also possible (Fig. S2). For example, the shape of the unimodal relationship between tree diversity and tree height depends on moose browsing intensity in Finnish boreal forest (Muiruri et al., 2015). A second example is where livestock grazing intensity inverts non-linear (saturating) temperature control of decomposition from weakly positive to strongly negative across global drylands (Maestre et al., 2022). Overall, many properties controlling decomposer physiology, such as pH or soil microclimate, can also be unimodal (hump-shaped), reflecting a zone of optimal conditions for microbial functioning and two sub-optimal extremes (e.g., Prescott, 2010). The shape of these relationships may be modified by large herbivores (Fig. S2).

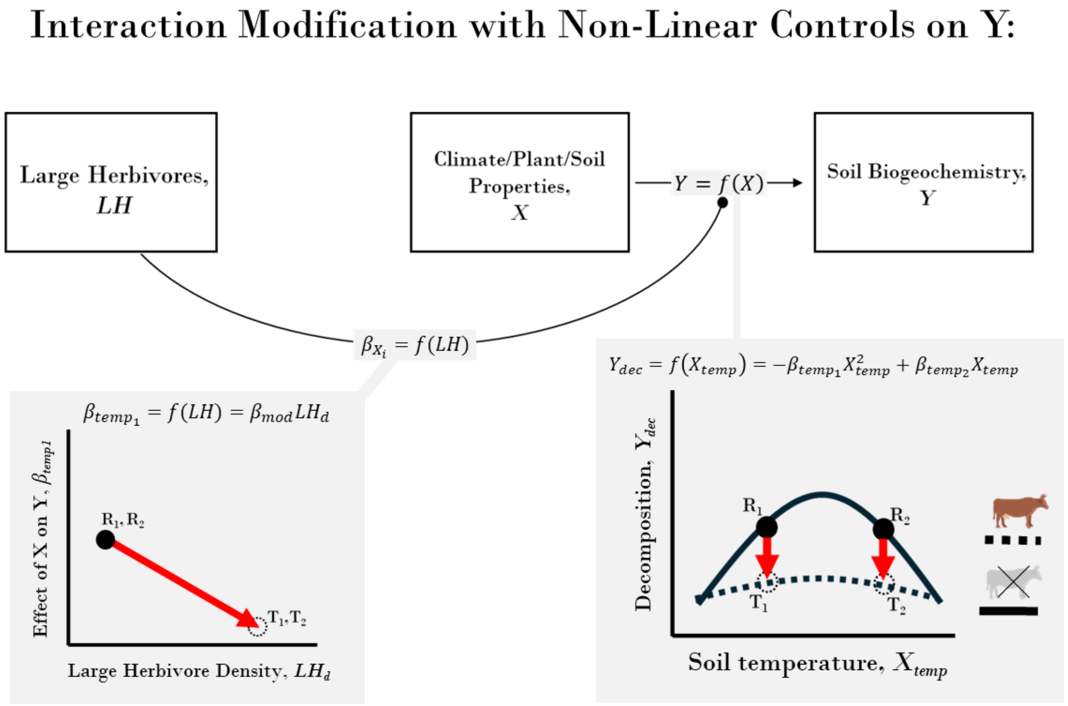

Figure S2. An interaction modification where control of an ecosystem process is non-linear, represented in network (directed acyclic graph), graphical, and statistical form. (A) An ecosystem process, *Y*, varies as a function of an abiotic or biotic control, *X*, according to the function $Y=f(X)$. A large herbivore treatment, *LH*, may then impact ecosystem processes, *Y*, via its relationship to the coefficient of one or more controls, β_{Xi}, according to a function $\beta_{Xi}=f(LH)$. (B,C) Dots, lines, arrows, and legends are consistent with Fig. S1. (B) For example, a coefficient of soil temperature, β_{temp1}, may vary as a function of large herbivore density, LH_d, according to a function $\beta_{temp1} = f(LH_d) = \beta_{mod} LH_d$, where β_{mod} is the coefficient of the herbivore effect on β_{temp1}. (C) Herbivore impacts on β_{temp1} may then shift temperature control of decomposition, Y_{dec}, according to a non-linear (e.g., unimodal) function.

Environmental Context

Environmental context can also influence the direction of herbivore direct effects on non-linear controls of ecosystem processes (i.e., equation 4: $\beta_{chain/mod}=f(EC)$), as with linear controls (Fig. 4a). For example, the direction of sheep trampling effects on soil moisture, depend on higher-order site variation in soil moisture (Schrama et al., 2013). Soil compaction by sheep waterlogs wet soils by reducing drainage, and exacerbates drought conditions in dry soil because compaction reduces water-holding capacity and increases runoff (Schrama et al., 2013; Fig. S3a,b). Unlike the linear case (Fig. 4a), nitrogen mineralization in this system is decreased over especially wet and dry sites because the same herbivore activity (trampling) creates soil conditions that compromise microbial functioning, but for different reasons depending on initial soil moisture (Fig. S3b).

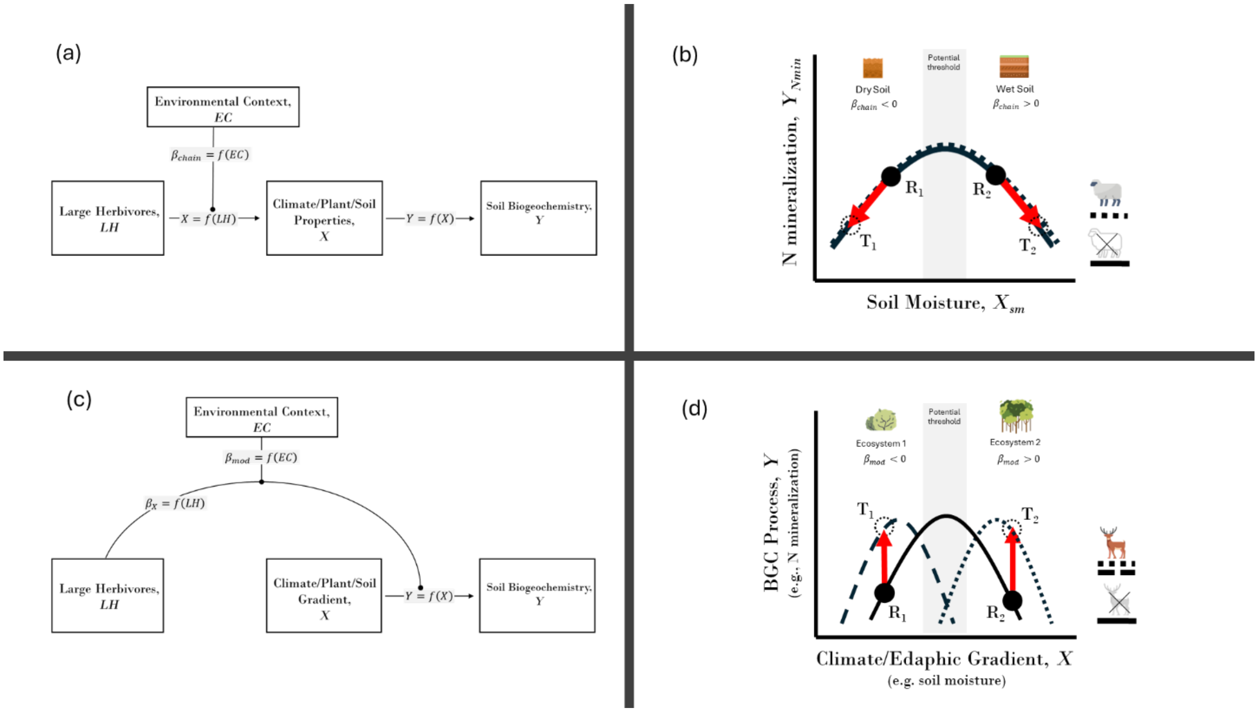

Figure S3. The role of environmental context in shaping large herbivore indirect effects on non-linear controls of ecosystem processes, via interaction chains and modifications. Point, line, arrow, and legend definitions are consistent with Fig S1. Variables representing environmental context can modify the coefficients of herbivore effects via interaction chain (A,B) and modification (C,D). (A,B) For example, variation in site-level soil moisture can modify the direction of large herbivore direct effects on soil moisture. (B) Since moisture control of N mineralization is non-linear (unimodal) herbivores decrease N mineralization via interaction chain at both wet and dry sites. (C) Environmental context can also constrain the direction of herbivore interaction modifications. (D) For example, in a case where a herbivores can modify the shape of unimodal soil functioning (e.g., N mineralization) by shifting microbial communities differently in different ecosystems.

As in the linear case presented in the main text (Fig. 4c,d), it may be possible for environmental context to influence the direction of interaction modifications of non-linear controls on ecosystem processes (Fig. S3c). However, to our knowledge, no attempts have been made to quantify this type of interaction structure. We therefore present a hypothetical example to illustrate how this pattern may present in the field. Consider again a system where a hump-shaped relationship exists between an edaphic gradient such as soil moisture or soil pH and a soil biogeochemical process such as nutrient cycling (Fig. S3d, solid line; Vivanco & Martiny, 2025). The hump shape reflects the physiological optimum of the decomposer community over the gradient. In this hypothetical system, large herbivores do not meaningfully alter site-level values along the *X* axis (i.e., no chain effect). Instead, the primary effect of large herbivores, via some mechanism (e.g., soil compaction, organic matter input, destruction of plant partners), is to alter microbial community composition from being generalist-dominated, with optimal physiological conditions along the midpoint of the *X*-axis gradient, to specialist-dominated with optimal conditions closer to the extremes (Abdul Rahman et al., 2021; Bradford et al., 2008; Winfrey et al., 2025). Thus, large herbivores modify the shape of the hump, including the position of the optimal condition along the soil gradient (Fig. S3d; Vivanco & Martiny, 2025). This is an example of environmental filtering via ecosystem engineering (Sanders & Frago, 2024). This shift, in turn, may be constrained by environmental context. In an ecosystem at the low end of the gradient, the optimum is shifted lower, because specialists adapted to this end of the gradient experience optimal activity at lower *X* than the suppressed generalists (Fig. S3d, dashed line). IN ecosystems at the high end of the gradient, the optimum is shifted higher, because specialists adapted to this region have a physiological optimum that is higher along the *X* axis than the generalists that are being suppressed (Fig. S3d, dotted line). Thus, in this hypothetical example a common herbivore treatment modifies the relationship $Y=f(X)$ (where, $\beta_{X2} = f(LH)$) based on a common mechanism that herbivores exert throughout their range (shift in microbial physiology via suppression of generalists, i.e., environmental filtering). The sign of this modification depends on environmental context (i.e., large-scale placement along edaphic gradient, $\beta_{LH} = f(EC)$). It is notable that in this interaction structure, local (plot scale) variation in *X* may result in entirely different shifts in *Y* across reference and treatment sites (i.e., R_1= strong increase; T_1=weak decrease; R_2=strong decrease; T_2=weak increase), despite ultimately sharing a single mechanism and interaction structure.

Case 2: Herbivore direct effects on ecosystem properties, $X = f(LH)$ (eq.2), are non-linear

The functional relationship between herbivore density, or more generally, the intensity of herbivory in space and time, can also be non-linear (Chen et al., 2013; Persson et al., 2007; Tuomi et al., 2021). This is commonly observed in agricultural systems where livestock densities can be easily controlled and range from zero to extremely high (Chai et al., 2019; Chen et al., 2013). Examples with wild large herbivores are limited, though examples exist with observational (Meyer et al., 2025) and experimental designs (Persson et al., 2007).

As with linear direct effects, the nature of non-linear herbivore direct effects can also be modified by environmental context (i.e., equation 4: $\beta_{LH} = f(EC)$). For example, in European boreal forest, the relationship between simulated moose browsing intensity and primary productivity of birch shifts from linear to increasingly unimodal over a gradient of site productivity index (Persson et al., 2007). In this case, intermediate browsing intensities substantially increasing primary productivity at productive sites, whereas browsing linearly decreases productivity at unproductive sites (Persson et al., 2007).

Overall, researchers should be aware of non-linear direct controls on ecosystem processes and non-linear herbivore direct effects, particularly at high densities. Non-linear effects present an obvious problem for projecting zoogeochemical patterns over landscapes. Fortunately, well-designed empirical studies can capture linear or non-linear effects (see Perspectives).

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