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REVIEW

The Mechanisms Underpinning Zoogeochemistry

Belowground effects of ground-dwelling large herbivores in forest ecosystems

Letícia Gonçalves Ribeiro[1,2] | **Mateus Melo-Dias**[1,2] | **Beatriz Maria Paccas Saraiva**[1,2] | **Nacho Villar**[1,3] | **Mauro Galetti**[1,2,4]

[1]Center for Research on Biodiversity and Climate Change, Institute of Biosciences, São Paulo State University (UNESP), Rio Claro, São Paulo, Brazil

[2]Laboratório de Biologia da Conservação (LABIC), Departamento de Biodiversidade, Instituto de Biociências, Universidade Estadual Paulista (UNESP), Rio Claro, São Paulo, Brazil

[3]Department of Aquatic Ecology, Netherlands Institute of Ecology, Wageningen, The Netherlands

[4]Kimberly Green Latin American and Caribbean Center, Florida International University (FIU), Miami, Florida, USA

Correspondence
Letícia Gonçalves Ribeiro
Email: leticia.goncalvesribeiro@gmail.com

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Abstract

1. Large terrestrial mammalian herbivores (LMHs) play a critical role in ecosystems, but the effects of these species on belowground zoogeochemistry in forest ecosystems remain poorly understood.
2. This study aimed to investigate the influence of LMHs on belowground processes in forest ecosystems. We synthesize current knowledge on how LMH species composition, physiology and feeding habits influence belowground litter and soil properties in boreal, temperate and tropical forests of the world through a systematic review.
3. Tropical forests host the highest diversity of LMHs, but are the least studied, with most species being threatened frugivorous ruminants and non-ruminants. Temperate and boreal forests are more studied and dominated by ruminant browsers or mixed feeder species.
4. The impact of LMHs shows high variation among forest types, but ruminants (Cervidae) tend to have negative effects on litter and soil properties in temperate and boreal forests, thereby decelerating nutrient cycling. Whereas LMHs non-ruminants (Suidae, Tapiridae and Tayassuidae) positively affect litter and soil properties in temperate and tropical forests.
5. Research on the effects of LMHs on litter and soil properties faces several challenges, including confounding factors, such as biotic and abiotic conditions, high contextual variability influenced by factors, such as forest type, seasonality and experiment time, and there is also a geographical bias, with most studies conducted in temperate forests, while research in tropical forests remains scarce.
6. LMHs are highly threatened by defaunation, which can disrupt ecosystem dynamics, highlighting the need to address research gaps. Long-term studies in tropical forests, particularly in South and Central America, Africa, India and Southeast Asia, are essential to understand the effects of LMHs on belowground properties.
7. While LMHs are hypothesized to reduce nutrient cycling in forest ecosystems, this effect appears to be highly context dependent underscoring the need for further research. Understanding these effects is critical for advancing ecological

knowledge and predicting climate change impacts on forest ecosystems. In addition, this can guide trophic restoration efforts and enhance ecosystem resilience.

KEYWORDS
boreal forests, moose, red deer, temperate forests, tropical forests, ungulates, wild boar, zoogeochemistry

1 | INTRODUCTION

Large terrestrial mammalian herbivores (LMHs) play a fundamental role in all ecosystems, yet we lack a better understanding of the uniqueness and differences of their effects in zoogeochemistry across different ecosystem types (Meyer & Leroux, 2023; Pringle et al., 2023; Schmitz et al., 2018). Most of our knowledge comes from grass-dominated ecosystems, where many plant species respond to LMH grazing with compensatory growth and, LMHs accelerate nutrient cycling when soils are highly fertile and/or at intermediate compaction and moisture conditions (Bakker et al., 2006; Harrison & Bardgett, 2004; Jia et al., 2018). In forests, LMHs are thought to selectively feed on palatable plant parts with lower C:N ratios and lignin content to facilitate digestion (Berzaghi et al., 2018; Venter et al., 2019). As a result, they promote herbivore-intolerant plants that produce low-quality litter and decelerate nutrient cycling rates (Bardgett & Wardle, 2003; Pastor et al., 1993). However, the effect of LMHs on belowground components of forests is not well understood (Kristensen et al., 2022; Maillard et al., 2021; Wardle et al., 2004). Most studies are based on nitrogen (N) dynamics and have been conducted in temperate and boreal forests, which are generally considered soil nutrient-poor ecosystems and dominated by cervids (Barrios-Garcia & Ballari, 2012; Sitters & Andriuzzi, 2019).

Although forests are generally considered nutrient-poor ecosystems in terms of soil fertility, boreal, temperate and tropical forests differ in many factors influencing nutrient cycling dynamics (Attiwill & Adams, 1993; Cronan, 2023). Temperate forests, for example, have deciduous, broadleaved and coniferous evergreen trees that shed leaves in winter, creating organic residues on the soil surface, however, decomposition and nutrient cycling are moderate due to climatic conditions (Adams et al., 2019). Boreal forests, in turn, are dominated by cold-tolerant evergreen conifers, with soil that are often moist and may be partially or fully frozen at northern latitudes (Gauthier et al., 2015). This slows down litter decomposition and nutrient cycling but results in more organic matter and nutrients stocks in soil (Prescott & Vesterdal, 2021). In contrast, tropical forests experience higher temperatures and abundant rainfall, leading to rapid litter decomposition and nutrient release for plant demand, with high turnover of nutrient cycling (Sanchez & Logan, 1992; Sayer et al., 2020). Furthermore, tropical forests, supporting more than 300 tree species per hectare (Gentry, 1988), are more biodiverse than temperate and boreal forests, which are often dominated by one or a few tree species (Thomas & MacLellan, 2009). Plant diversity can enhance nutrient cycling by enabling species to exploit different niches, increasing nutrient uptake and reducing losses through leaching (Hobbie, 1992; Hooper & Vitousek, 1998).

Differences in nutrient cycling among forest types, along with factors, such as LMH species composition, feeding habits, physiology and behaviour, challenge the generalization that LMHs decelerate nutrient cycling in forest ecosystems (Sitters & Andriuzzi, 2019). Regardless of forest type, our understanding of how LMHs affect soil zoogeochemistry remains limited (Andriuzzi & Wall, 2017; Leroux & Schmitz, 2025; Meyer & Leroux, 2023; Tomita et al., 2025). In this context, this study aims to investigate the effects of LMHs on nutrient cycling in forest ecosystems and identify overall patterns and research gaps. Specifically, we (I) synthesize LMH species composition, physiology and feeding habits across boreal, temperate and tropical forests; (II) assess the effects of LMHs on litter and soil properties to identify general patterns in these forest types; and (III) highlight research challenges and propose future directions.

2 | MATERIALS AND METHODS

We conducted a systematic literature review following the PRISMA framework (Page et al., 2021). We searched the Web of Science, Scopus and Google Scholar using the following keywords: (1) "herbivor*" combined with "large" OR "mammal*"; (2) "soil"; (3) "litter"; (4) "temperate"; (5) "boreal"; (6) "tropical"; (7) "terrestrial"; and OR "terrestrial mammal*"; (2) "soil"; (3) "litter"; (4) "temperate"; (5) "boreal"; (6) "tropical"; (7) "forest". Peer-reviewed studies published until 2024 in English, Portuguese and Spanish were included. A title search was performed for all keyword combinations, yielding 218 studies (Appendix S1; Figure S1). Titles were screened for relevance, followed by a review of the abstracts. These studies were then filtered to include only those conducted in terrestrial ecosystems that experimentally examined the effects of LMHs on litter and soil properties, either through natural or exclusion experiments. Literature reviews and studies focusing exclusively on large domestic herbivores, such as cattle, horses and sheep, were excluded, although studies evaluating the effects of domestic and wild herbivores separately were included considering only wild LMHs results. The exclusion criteria are detailed in Appendix S1.

A total of 54 studies were included in our systematic review, comprising 48 exclusion experiments and only six natural exclusions (Appendix S2). Given the relatively small number of studies meeting our inclusion criteria, a robust quantitative meta-analysis was not feasible. Therefore, we focused on compiling directional effects (positive, negative and null), highlight general result patterns and identify knowledge gaps, while avoiding over-interpretation of limited data.

We considered as large herbivores those weighing more than 10 kg (Tanentzap & Coomes, 2011). We then reviewed the selected studies in detail and retrieved the following information: (1) forest type (temperate, boreal or tropical); (2) geographic location; (3) LMH species; (4) native or invasive alien species; (5) litter and soil properties evaluated; (6) negative, null or positive effect of LMHs on litter and soil properties evaluated (see Appendix S2). To identify general patterns, we selected the litter and soil properties most frequently reported across the reviewed studies. We categorized the effects of LMHs on each variable as positive, negative or null. An effect was classified as positive when the presence of LMHs was associated with a statistically significant increase in the measured variable; negative when there was a significant decrease; and null when no significant effect was detected. This classification approach was necessary because the reviewed studies reported their results using different methodologies, for example, comparing exclusion and control plots, or modelling litter and soil responses as functions of LMH presence/absence alongside other environmental factors. Appendix S2 lists all studies included in our systematic review, while Appendix S3 (Figures S1 and S2) indicates whether the effects of LMHs were positive, null or negative, and which study reported each effect.

Finally, to compile LMHs species composition in boreal, temperate and tropical forest habitats, we made a list using the IUCN terrestrial mammal dataset (IUCN (International Union for Conservation of Nature), 2025), filtering species with a body mass of more than 10 kg that occur in forests. Species were considered if they occupy forest habitat types according to the IUCN classification scheme. Information on feeding habits and body weight was obtained from Wilson and Mittermeier (2011) and the IUCN Red List (2025) (see Appendix S4). This study did not involve fieldwork or direct experimentation on animals. Therefore, no ethics approval from an animal ethics committee or permits for fieldwork were required.

3 | RESULTS AND DISCUSSION

3.1 | Differences of LMHs according to forest types

3.1.1 | Physiology and feeding habits of LMHs: Key concepts

LMHs depend on the fermentation of fibrous plant components by intestinal microbes, as they are unable to break down plant fibres through auto-enzymatic processes (Stevens & Hume, 1995). Most LMHs have a foregut that can be classified as ruminant or non-ruminant (Munn et al., 2008). Ruminants (e.g. Cervidae and Bovidae) have a stomach consisting of four compartments, whereas non-ruminants (e.g. Suidae, Tapiridae and Elephantidae) have a simple stomach (Clauss & Hofmann, 2014). But in terms of the belowground effects of LMHs, why do these physiological differences matter? These differences can influence diet and habitat selection, which in turn affect their interactions with belowground dynamics, such as nutrient cycling (Cromsigt et al., 2009; Gordon, 2003; Spitzer et al., 2020). Ruminants typically exhibit selective feeding, preferring more palatable plant parts with a low C:N ratio, which reduces the chances that ingested food will pass through the rumen incompletely digested (Demment & Van Soest, 1985). This process results in more efficient fibre digestion in ruminants compared with non-ruminants. Moreover, herbivores that consume N-rich forage tend to return more labile nutrients to the soil, particularly through urine (Sitters et al., 2017). In contrast, non-ruminants compensate for less efficient nutrient extraction by having a faster throughput rate on low-quality foods, allowing them to consume more of such foods (Duncan et al., 1990). As a result, non-ruminants are more efficient than ruminants at processing low-quality food (higher fibre content) (van Wieren, 1996). However, herbivores that consume low-quality food with a high C:N ratio must extract as much N as possible for their metabolic needs and, therefore tend to return nutrient-poor faeces to the soil (Sitters et al., 2017). Consequently, the contrasting digestive strategies of LMHs influence the return of nutrients to the soil, thereby affecting nutrient cycling.

Ruminants and non-ruminants are found in all forest types, but both generally focus on grass, browse or fruit as their primary food source, forming a continuum of grazer/browser/frugivore dynamics (Bodmer, 1990; Hofmann, 1989). Grazers (e.g. black wildebeest, *Connochaetes gnou*) focus on monocotyledonous species and are typically found in open grasslands, where these resources are abundant and spatially continuous (Fritz & Loison, 2006; Smit, 2011). As a result, LMHs often form large groups, not only to efficiently exploit available resources but also as a strategy to reduce predation risk (Creel et al., 2014). Browsers (e.g. moose, *Alces alces*) are herbivores that primarily feed on dicotyledonous species (Gordon & Prins, 2019). They are more common in forested habitats, where browse resources tend to be patchy and spatially dispersed. As a result, browser species typically adopt a hiding strategy and live in smaller groups compared with those inhabiting open environments (Fritz & Loison, 2006). An intermediate category, known as mixed feeders (e.g. fallow deer, *Dama dama*), consumes a combination of monocots and dicots, depending on factors, such as seasonality and resource availability (Gebert & Verheyden-Tixier, 2001).

While temperate and boreal forests support high primary production in the shrub layer, and grasslands are dominated by field-layer grasses, tropical forests are characterized by a closed canopy that limits primary productivity in both the ground and shrub layers (Gilliam, 2007; House & Hall, 2001; Smirnova et al., 2017). As a result, fruit fall becomes the most abundant and important food source for LMHs in these ecosystems (Terborgh, 1986; Villar et al., 2022). Consequently, frugivorous LMHs (e.g. lowland tapir, *Tapirus terrestris*) are more common in tropical forests, feeding primarily on readily available fruits and seeds (Jordano, 2014). Ruminants use the reticulorumen to degrade seed defences, whereas non-ruminants rely on digestive and dental adaptations to predate seeds (Bodmer, 1989; Janzen, 1981). Although primarily frugivorous, these species may also consume leaves, seedlings, shrubs and herbs, and, in the case of peccaries (e.g. *Tayassu pecari*, *Dicotyles tajacu*), roots, particularly when fruit is scarce (Davies et al., 2001; Keuroghlian & Eaton, 2009). In response to seasonal fluctuations in fruit availability, frugivorous LMHs often shift towards browsing diets during fruit-scarce periods (Akkawi et al., 2020; Bodmer, 1990; Branan et al., 1985).

Understanding the diversity of physiological and feeding habits among LMHs is essential to unravel their roles as agents of nutrient redistribution (Danell et al., 2006). These traits not only mediate the quality and quantity of resources returned to the soil through dung and urine but also determine foraging behaviour and, consequently, the physical impacts of LMHs on the environment (Pastor & Cohen, 1997; Trepel et al., 2024; Wolf et al., 2013).

Body mass is also important because as it increases, the metabolic demand for food increases, so LMHs expand their diet to include lower-quality food (Demment & Van Soest, 1985). In addition, larger body size increases gut capacity and food retention time, which improves nutrient assimilation (Munn et al., 2008). Body size not only shapes herbivore foraging strategies but also affects the quantity and quality of nutrient inputs belowground, with cascading effects on soil fertility and plant chemistry and community dynamics (Leroux et al., 2020; Sitters & Olde Venterink, 2021). Furthermore, species with larger body mass are more susceptible to local or regional extinction because they are more easily hunted and affected by habitat loss (Dirzo et al., 2014; Young et al., 2016).

3.1.2 | LMHs species composition in forests

We document 167 LMHs species in forests, with approximately 78% (130 species) occurring in tropical forests, 33% (56 species) in temperate forests and 7% (12 species) in boreal forests (Appendix S4). Boreal forests are primarily dominated by species of Cervidae, ruminants whose feeding habits are predominantly browsers (Figure 1b). The species with higher body mass is the moose, whose male body

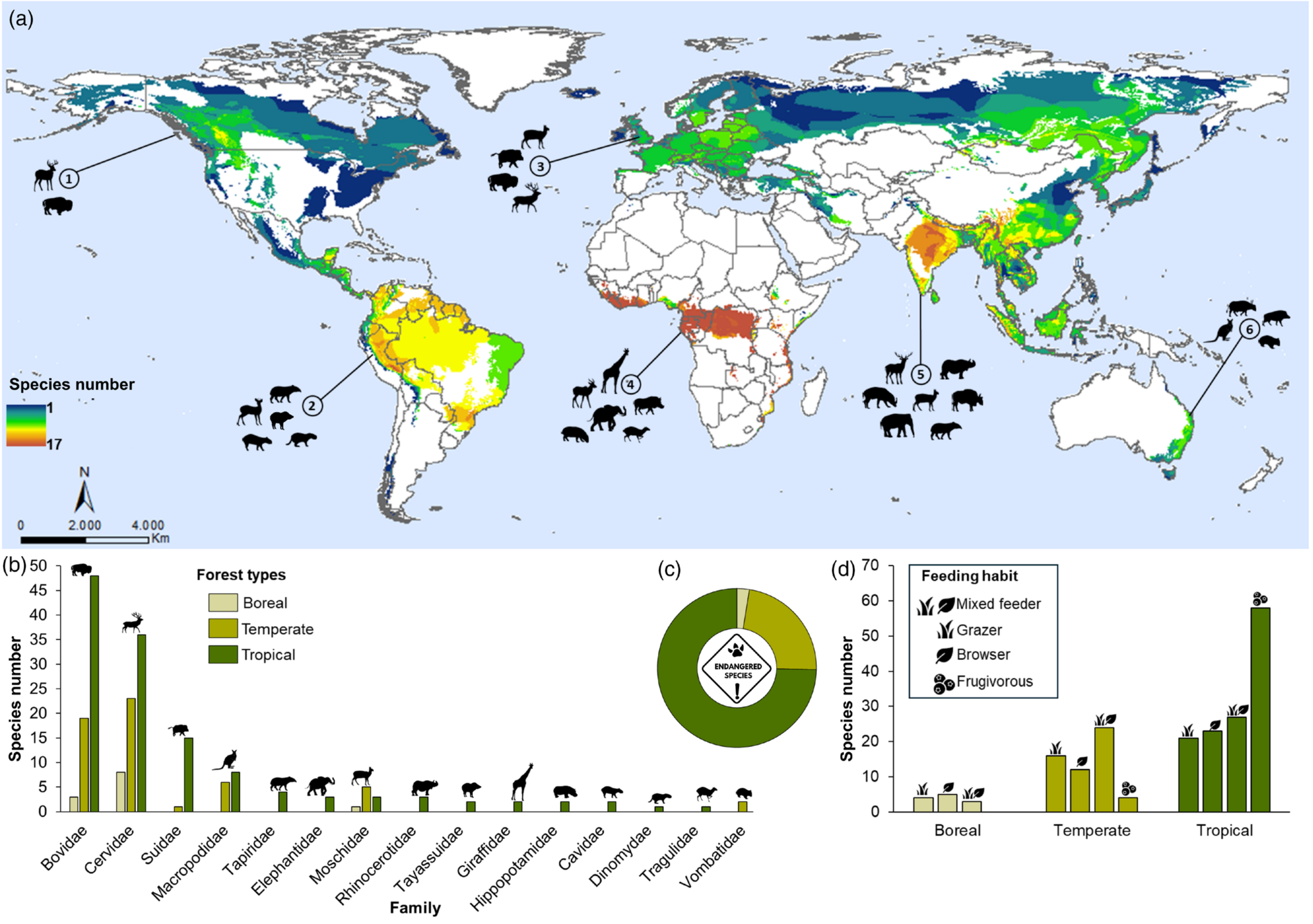

FIGURE 1 Species richness distribution of ground-dwelling large mammalian herbivores (LMHs) in forests (a). Species icons represent the families present in the biogeographical realms: (1) Nearctic, (2) Neotropical, (3) Palearctic, (4) Afrotropical, (5) Indomalayan and (6) Australasian. Panels show LMHs families occurring in forests (b); threatened species (vulnerable, endangered, critically endangered) according to the IUCN Red List (c) and feeding habits of LMH species in forests (d). Credit: PhyloPic icons.

mass can reach 450 kg (Appendix S4). In temperate forests, species of Bovidae and Cervidae are also common, though these species tend to be mixed feeders (Figure 1d). The species with higher body mass is the North American bison (*Bison bison*) weighing up to 730 kg (Appendix S4).

In tropical forests, Bovidae and Cervidae are the primary LMH species, along with Suidae, and 44% are frugivores (Figure 1d). Tropical forests store approximately 40% of the world's terrestrial carbon, and frugivorous LMHs (arboreal and ground-dwelling) are presumed to play a crucial role in the dispersal of large seeds which grow into trees that store more carbon (Dixon et al., 1994; Bello et al., 2015; Berzaghi et al., 2018; Brodie et al., 2024). Tropical forests are also home to the largest LMHs by body mass, such as the African forest elephant (*Loxodonta cyclotis*, 4350 kg) and the Indian rhinoceros (*Rhinoceros unicornis*, 2000 kg), which are found in Africa and Asia, respectively. In the Neotropics, LMHs have a smaller body mass, with the Baird's tapirs (*Tapirus bairdii*) being the largest, reaching 350 kg, while most species, including peccaries and cervids, weigh between 20 and 32 kg (Appendix S4). The loss of mega-herbivores in the Neotropics was higher than in any other biogeographic realm, and it has been theorized that humans or climate change, or their interaction, caused extinctions of these species (Antonelli, 2022; Galetti et al., 2018; Raczka et al., 2018). Nearly half of tropical forest LMH species are classified as threatened by the IUCN Red List (2025) (Figure 1c). As a result, these species occur at low densities, complicating efforts to accurately assess their ecological impacts (Bogoni et al., 2020). In many habitats, local extinctions may have occurred, necessitating studies in areas where populations remain relatively intact to better understand their ecological roles (Brodie et al., 2021; Naughton-Treves et al., 2005).

Despite the high diversity of LMHs in forest ecosystems, only 14 species were mentioned across the 54 studies included in our systematic review. This represents less than 10% of the total LMH species richness known to occur in the world's forests. Most studies focus on cervids (moose, red deer and white-tailed deer) or wild boar as dominant species and are mostly conducted in temperate forests, with few in tropical forests and none addressing the effects of mega-LMHs in Asia and Africa on belowground properties of forests (Figure 2a). This highlights a significant knowledge gap in tropical forests and the lack of information on how different LMH species compositions may influence belowground properties, even within the same forest type.

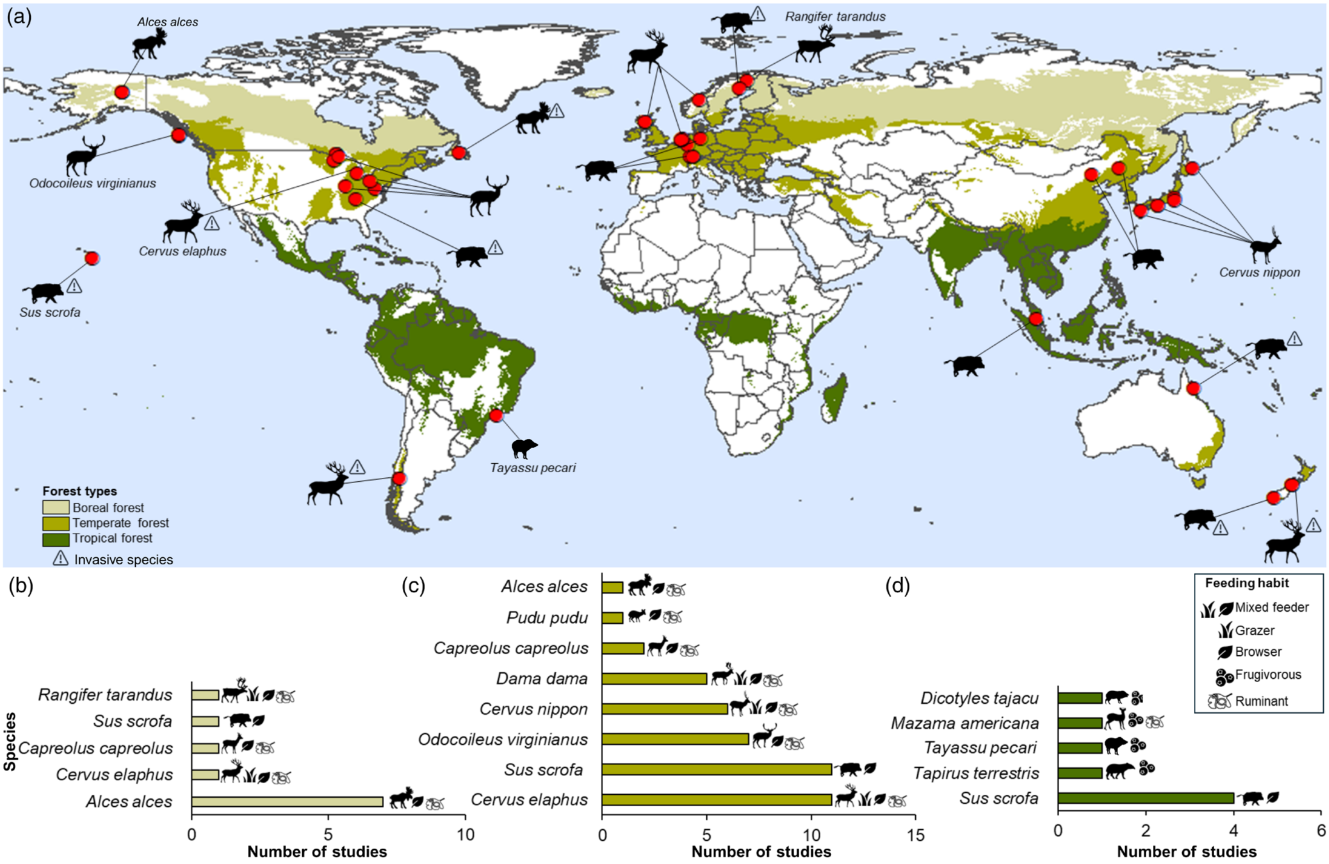

FIGURE 2 Global distribution of studies evaluating the effects of ground-dwelling large mammalian herbivores (LMHs) on litter and soil properties in forests (a); main LMHs cited in reviewed studies for boreal (b), temperate (c) and tropical (d) forests, along with their feeding habits. Red circles indicate the locations of reviewed studies. The map features icons representing the primary LMH for each study. Credit: PhyloPic icons.

3.1.3 | LMHs effects on nutrient cycling in forests

Temperate and boreal forests are dominated by browsing LMHs' ruminant species and are typically nutrient-poor, low-productivity ecosystems (Attiwill & Adams, 1993; Cronan, 2023). In these environments, long-term selective browsing has accelerated ecological succession, leading to the dominance of woody plants with low litter quality (Pastor et al., 1993; Ramirez et al., 2021). These forests support relatively few species of browsers that consume a small fraction of plant biomass, resulting in a limited return of labile nutrients through excreta (Harrison & Bardgett, 2004). This nutrient return is insufficient to offset the negative effects of LMHs' induced changes in plant composition and quality (Wardle et al., 2002). As a result, browsing LMHs are expected to decelerate nutrient cycling in these forest ecosystems (Pastor et al., 1998; Sitters & Andriuzzi, 2019).

In contrast, what are the effects of frugivorous LMHs on nutrient cycling in tropical forests? Some studies showing the effects of LMHs on belowground properties are based on arboreal species, such as primates, or consider all mammalian species (Feeley & Terborgh, 2005; Losada et al., 2023; Sobral et al., 2017). For example, a study conducted in a tropical forest in Venezuela shows that soil nutrient availability decreases with higher densities of folivorous howler monkeys (*Alouatta seniculus*) (Feeley & Terborgh, 2005). These results are also explained by selective feeding on plants with a low C:N ratio, resulting in poor litter quality and reduced nutrient return to the soil (Bardgett & Wardle, 2003; Wardle et al., 2001). However, studies of the effects of ground-dwelling LMHs on soil properties indicate that LMHs have positive effects on ammonium availability and pH, suggesting that they may accelerate nutrient cycling in tropical forests (Brearley et al., 2021; Villar et al., 2020).

3.2 | LMHs effect on belowground properties in forests

3.2.1 | Boreal forests

We identified nine studies that evaluated the impact of LMHs on litter and soil properties in boreal forests. Eight of these studies focused on moose (*A. alces*), a ruminant browser species. Adult males can weigh over 450 kg, while females typically range from 275 to 360 kg, and moose are generally solitary animals except for females accompanied by their offspring (Niedziałkowska et al., 2022). Moose generally have a negative impact on litter, reducing biomass, C and N content (Figure 3a) (Kielland & Bryant, 1998; Pastor et al., 1998). They also have negative impacts on soil chemical properties, as reduction in N, C, cation exchange capability, ammonium and nitrate (Figure 3b) (Pastor et al., 1993; Pastor et al., 1998; Stark et al., 2010). This can be attributed to the cascading effects of reduced litter quality and quantity resulting from selective browsing of palatable plants (Carline et al., 2005; Niwa et al., 2011; Pastor et al., 1993). These changes can also lead

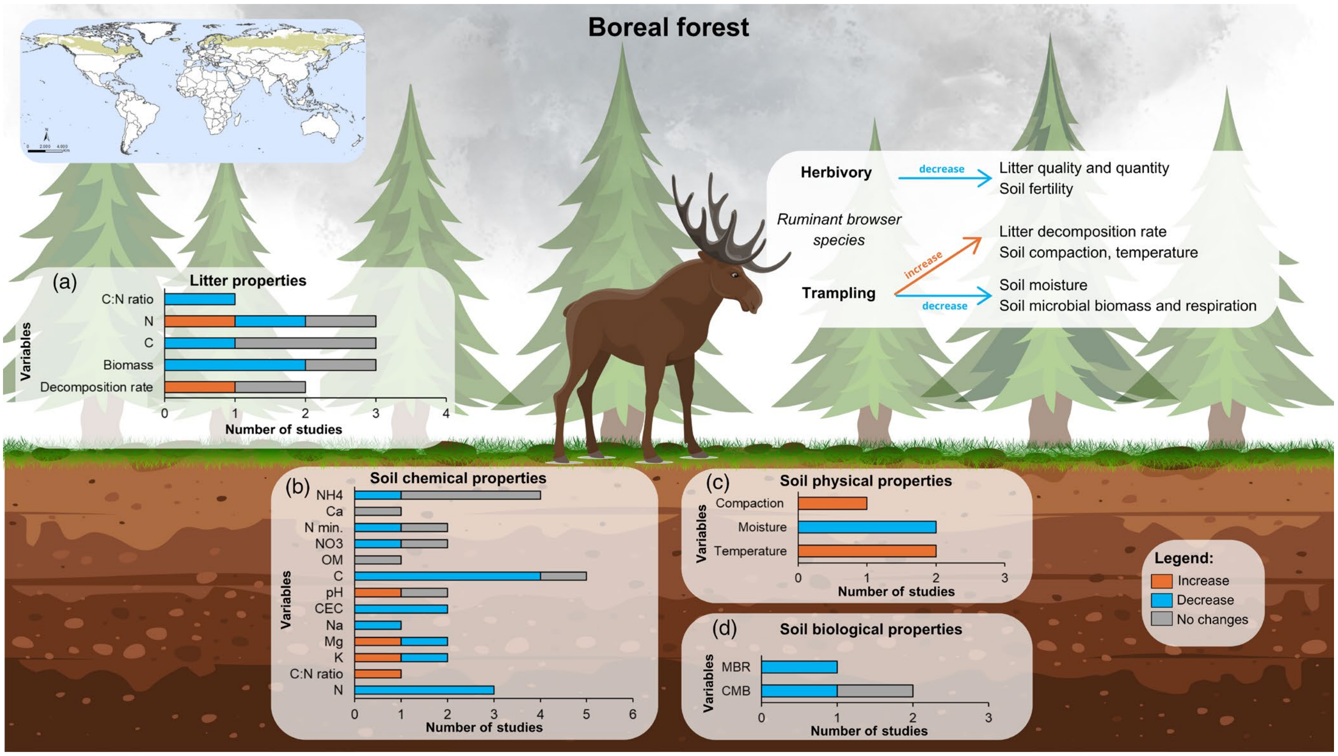

FIGURE 3 Effect of ground-dwelling large mammalian herbivores (LMHs), principally moose (*Alces alces*) on litter (a), soil chemical (b), physical (c) and biological (d) properties in boreal forests. CBM, carbon of microbial biomass; MBR, microbial basal respiration; N min., nitrogen mineralization; OM, organic matter. Orange indicate an increase, blue a decrease, and grey effects indicate no change in the measured variable in the presence of LMHs. Created with CanvaPro.

to effects on soil biological properties, with negative effects of LMHs on microbial biomass and respiration (Figure 3d) (Pastor et al., 1998). Decreases in N, C and other essential soil nutrients directly restrict the resources available to microbial communities, which depend on these elements for growth and metabolic activity (Harrison & Bardgett, 2004).

Not only can feeding habits but also trampling by LMHs affect belowground conditions, especially given the considerable body mass of moose (Tuomi et al., 2021). There is an increase in soil temperature and compaction (bulk density) while decreased soil moisture is promoted by moose in boreal forests (Figure 3c) (Appendix S3; Figure S1) (Kielland & Bryant, 1998; Kolstad et al., 2018). Trampling can cause soil compaction, resulting in increased bulk density, which decreases soil porosity and consequently soil oxygen levels (Long et al., 2017). In addition, trampling can remove forest floor vegetation, leaving the soil exposed, which increases temperature and decreases moisture (Elledge et al., 2010; Kumbasli et al., 2010). These changes in soil physical properties can hinder seedling establishment, reduce soil oxygen levels and negatively affect invertebrate abundance and microbial activity (Leroux et al., 2020).

3.2.2 | Temperate forests

Most of the peer-reviewed studies are conducted in temperate forests (72.2%, $n=39$) (Figure 2a). There are two main LMHs focal species in the literature, the wild boar (*Sus scrofa*) ($n=14$), a non-ruminant browser omnivorous species, and the red deer (*Cervus elaphus*) ($n=14$), a ruminant mixed feeder ungulate (Figure 2c) (Gordon & Prins, 2019). The wild boar is native to Eurasia and is considered a widespread invasive alien species in other parts of the world, such as Oceania and America (Barrios-Garcia & Ballari, 2012). Adult males' body mass averages 75–100 kg, while females reach approximately 60–95 kg, and they typically live in social groups ranging from 5 to 10 individuals (Scandura et al., 2022). Although generally classified as a browser species in forest ecosystems, their diet may include seeds, fruits, roots and even animal matter depending on local conditions and seasonal food availability (Bodmer, 1990; Gordon & Prins, 2019). Given this dietary flexibility, they can be positioned along a browser–frugivore continuum or classified as omnivorous depending on seasonality and habitat (Sridhara et al., 2016). The red deer is native to the temperate and boreal forests of Europe, but has been introduced to other regions, including the United States, Argentina, Chile, New Zealand and Australia, where it is now considered an invasive species (Lovari et al., 2018). Male red deer body mass ranges from 100 to 220 kg, while females weigh between 55 and 130 kg. The species is gregarious, typically forming groups of five to seven individuals in forested areas (Mattioli et al., 2022). In the reviewed studies, both species are present in their native geographic distribution and in localities where they are considered invasive (Figure 2a).

Literature generally predicts that these LMHs reduce both the quantity and quality of litter due to selective feeding of palatable plant species (Pastor et al., 1993; Ramirez et al., 2021; Wardle et al., 2004). As in boreal forests, ruminant cervid LMHs reduce litter C, N and biomass in temperate forests (Figure 4a) (Appendix S3; Figure S1) (Ellis & Leroux, 2016; Ramirez et al., 2019). They also reduce litter decomposition rates by decreasing litter quality and increasing lignin content (Chollet et al., 2021; Kasahara et al., 2016). However, contrasting results have been reported, as LMHs can also accelerate litter decomposition and reduce litter biomass through trampling (Figure 4a) or, specifically, via grubbing by wild boar (Figure 5a). This physical disturbance fragments the litter and facilitates colonization by decomposer microorganisms thereby potentially increasing nutrient availability and influencing ecosystem nutrient cycling (Ramirez et al., 2021; Singer et al., 1984).

The reviewed studies largely focus on soil chemical properties in temperate forests, where the effects of LMHs exhibit greater variability (Figure 4b). However, there are predominantly negative effects of LMHs on soil chemistry from ruminants, such as reductions in N, C, P, K, nitrate and ammonium. These results are usually attributed to shifts in litter quality because of herbivory, eventually decelerating nutrient cycling (Furusawa et al., 2005; Gass & Binkley, 2011; Mohr et al., 2005). However, LMHs also have a positive effect on soil pH, nitrate, ammonium, nitrogen mineralization and organic matter (Bressette et al., 2012; Harrison & Bardgett, 2004; Stritar et al., 2010). Usually, the explanation for such a positive effect is that herbivory by LMHs reduces plant density, which in turn reduces nutrient demand and uptake by plants, leaving more nutrients available in the soil (Kielland et al., 1998; Bressette et al., 2012; Tokumoto et al., 2024). Additionally, dung and urine inputs from herbivores provide a reliable source of nutrients for the soil (Maillard et al., 2021; Wardle et al., 2001). These mechanisms highlight how LMHs can, under certain conditions, enhance nutrient availability and promote soil fertility in temperate forests.

In contrast to studies where LMHs are predominantly ruminants, studies with wild boar, that is a non-ruminant species, show trends towards positive effects on soil chemistry (Figure 5b). This LMH increases soil C, Ca, P, ammonium and nitrate (Liu et al., 2020; Sun et al., 2024; Wirthner et al., 2012). These could be explained by grubbing activities by wild boar, where bioturbation can promote soil aeration, and mixing litter in the soil, incorporating organic matter and enhancing microbial activity, and consequently releasing nutrients for soil (Mohr & Top, 2005). But this nutrient release can also accelerate the nutrient leaching process depending on other soil properties, such as texture (Singer et al., 1984).

There are also contrasting effects with LMHs predominantly ruminants (cervids) and non-ruminants (wild boar) in relation to soil physical properties. Whereas cervids increase soil compaction due to trampling and their relatively high body mass (Figure 4c), wild boar reduce compaction through grubbing, which promotes bioturbation and enhances soil mixing (Figure 5c) (Appendix S3; Figure S1) (Kumbasli et al., 2010; Sun et al., 2024). Lastly, the

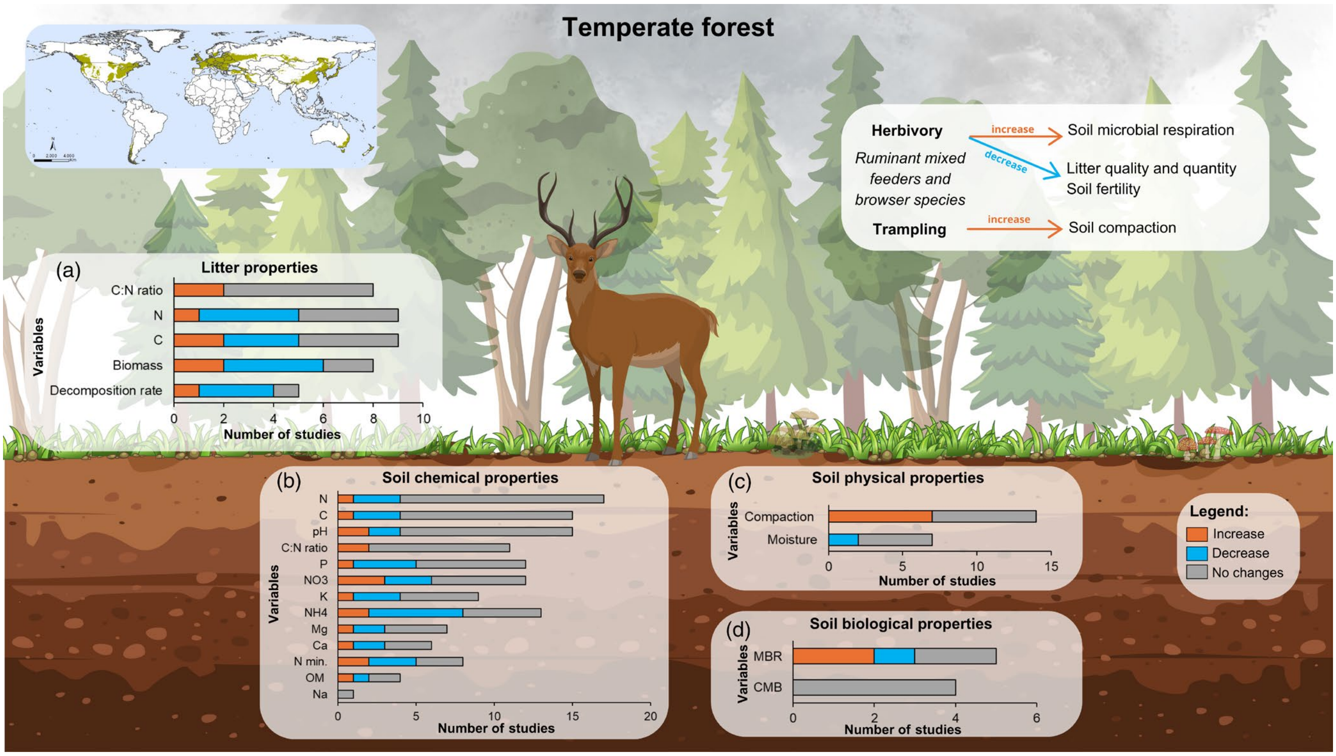

FIGURE 4 Effect of ground-dwelling large mammalian herbivores (LMHs), principally cervids (*Cervus elaphus* and *Odocoileus virginianus*) on litter (a), soil chemical (b), physical (c) and biological (d) properties in temperate forests. CBM, carbon of microbial biomass; MBR, microbial basal respiration; N min., nitrogen mineralization; OM, organic matter. Orange indicate an increase, blue a decrease, and grey effects indicate no change in the measured variable in the presence of LMHs. Created with CanvaPro.

effect of LMHs on soil biological properties is less studied. Existing evidence suggests a variable impact of LMHs, particularly ruminants, on soil microbial respiration, with increases observed in nutrient-rich (N-rich) environments and decreases in nutrient-poor conditions (Figure 4d) (Popma & Nadelhoffer, 2020). In high-nutrient sites, plants tolerate herbivory by enhancing productivity and producing N-rich litter, which reduces the need for microbial respiration (Frey et al., 2014). In contrast, under low-nutrient conditions, litter is N-poor, prompting microbes to increase respiration to acquire nitrogen. In the case of non-ruminant LMHs, wild boar increases soil microbial biomass carbon and microbial respiration, whereas these results are explained by a faster turnover rate of C in grubbed soils (Figure 5d) (Risch et al., 2010; Wirthner et al., 2012).

3.2.3 | Tropical forests

We found only five studies conducted in tropical forests, with the wild boar ($n=4$) being the main LMH investigated (Figure 2d). Three of these studies were conducted in areas where the species is invasive, and one within its native range. A study in South America presents native LMHs, mentioning the white-lipped peccary (*T. pecari*), lowland tapir (*T. terrestris*), collared peccary (*D. tajacu*), red brocket deer (*Mazama americana*) all considered frugivorous, and, with the exception of the red brocket deer, all are non-ruminant (Davies et al., 2001; Villar et al., 2020). The white-lipped and collared peccaries are gregarious species, typically forming groups of 30–150 and 5–50 individuals, respectively (Wilson & Mittermeier, 2011). Most of these species have a body mass between 26 and 36 kg, except for the lowland tapir, which is considerably larger, reaching up to 300 kg (Paglia et al., 2012).

There is sparse information about the effect of LMHs on litter in tropical forests, with only one study showing a negative effect of LMHs on litter moisture due to higher weathering exposure caused by wild boar grubbing (Figure 6a) (Elledge et al., 2010). Regarding soil chemical properties, LMHs can have negative effects, such as reductions in Ca, Mg and K, which may be associated with nutrient release through grubbing, a disturbance that can also promote leaching (Figure 6d) (Long et al., 2017). Otherwise, different from temperate and boreal forests, there is a trend of positive effects of LMHs on soil chemistry, such as an increase in pH, C, N, P, ammonium and organic matter (Brearley et al., 2021; Long et al., 2017; Villar et al., 2020) (Appendix S3; Figure S1). In the case of frugivorous LMHs (e.g. tapirs and peccaries), they use areas with high fruit production more intensively, creating hotspots for nutrient recycling and increasing nitrification rates (Bodmer & Ward, 2006; Keuroghlian & Eaton, 2009; Villar et al., 2022). As suids, peccaries have a similar habit to wild boar, in which, through their rooting and grubbing they promote soil bioturbation, reducing soil compaction (Figure 6c) and increasing soil oxygen diffusion, thereby stimulating microbial activity and nutrient release (Beca et al., 2022; Long et al., 2017).

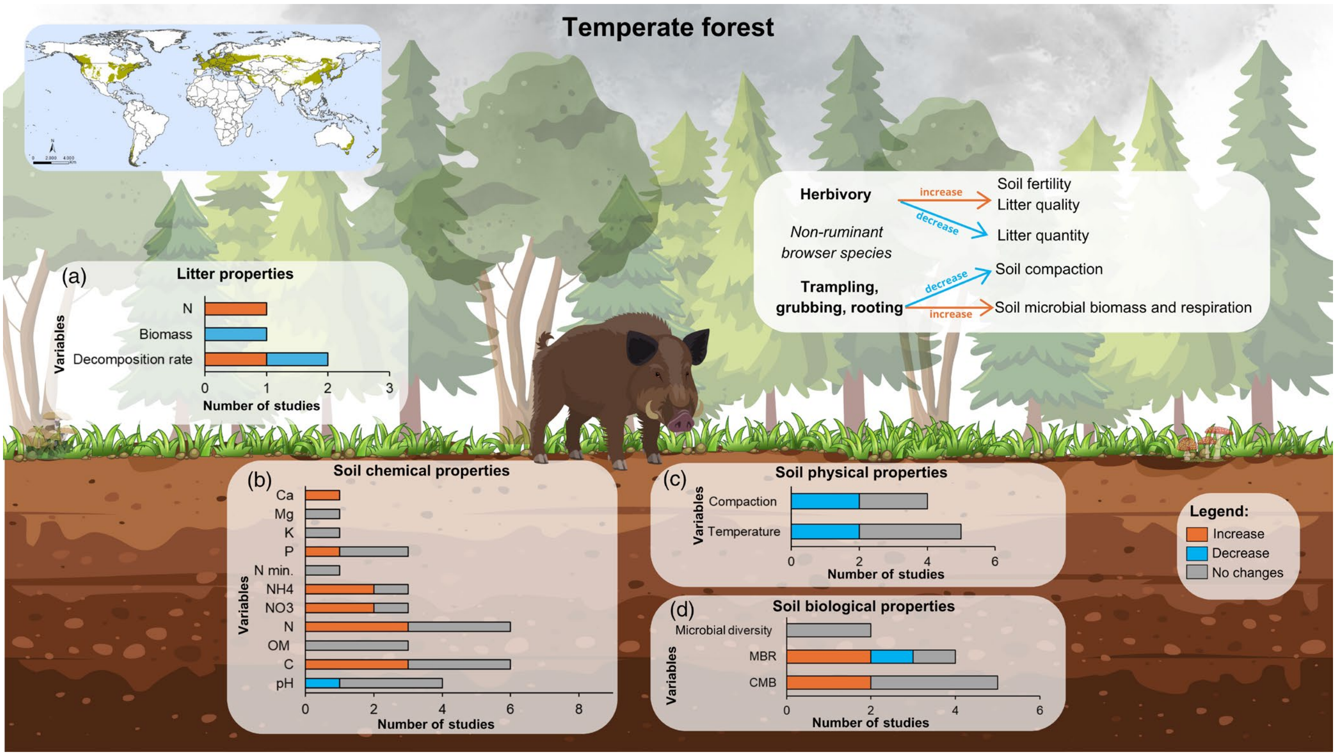

FIGURE 5 Effect of ground-dwelling large mammalian herbivores (LMHs), wild boar (*Sus scrofa*) on litter (a), soil chemical (b), physical (c) and biological (d) properties in temperate forests. CBM, carbon of microbial biomass; MBR, microbial basal respiration; N min., nitrogen mineralization; OM, organic matter. Orange indicate an increase, blue a decrease, and grey effects indicate no change in the measured variable in the presence of LMHs. Created with CanvaPro.

3.3 | Research frontiers

3.3.1 | Confounding factors

Among the 54 studies reviewed, nearly all reported at least one null effect of LMHs on litter or soil properties. Notably, one study reported exclusively null effects (Relva et al., 2014), while in several other studies, LMHs had null effects for most measured variables, occurring in both ruminant and non-ruminant species (Brearley et al., 2021; Elledge et al., 2010; Ellis & Leroux, 2016; Kolstad et al., 2018). However, does this truly imply that LMHs have no impact on these properties? Litter and soil interact with numerous abiotic and biotic factors, complicating the isolation of LMHs' effects. Three primary factors drive litter decomposition: climate > litter chemistry > biota (Aerts, 1997). For soil properties, the controlling factors are even more intricate: macroclimate > land surface age > parent material > microclimate > topographic position > biota (Sollins, 1998). Biota represents only a minor component of this complex system, suggesting that the influence of LMHs may be to some extent context dependent and masked by other, more dominant environmental factors.

3.3.2 | Context dependency

Based primarily on studies in temperate and boreal forests, with limited research from tropical forests (Berzaghi et al., 2018), it is challenging to conclude that LMHs have a consistent impact on decelerating nutrient cycling across forest ecosystems. With a higher number of studies, we found proportionally more variability in the effect of LMHs. Even within temperate and boreal forests, where vegetation and climate conditions are more similar to each other than those in tropical forests, the effects of LMHs on litter and soil properties are variable. In some cases, LMHs exhibit varying effects across different sites or seasons within the same study area (Gass & Binkley, 2011; Stritar et al., 2010; Wardle et al., 2001). Findings suggest that LMHs may decelerate (Chollet et al., 2021; Wardle et al., 2002), accelerate (Kielland & Bryant, 1998; Tokumoto et al., 2024) or have an ambiguous impact on nutrient cycling (Popma & Nadelhoffer, 2020). This variability indicates a strong dependency on context, as the dynamics of nutrient cycling differ across forest types due to abiotic factors (e.g. climate, parent rock material and terrain) and biotic factors (e.g. LMH richness, body mass, feeding habits and social behaviour), which together influence the extent to which LMHs affect litter and soil (Schrama et al., 2013; Adams et al., 2019; Sitters & Andriuzzi, 2019; Meyer & Leroux, 2024).

3.3.3 | Exclusion time

Another factor influencing the variability in the effects of LMHs on litter and soil, or the absence of such effects, is the duration of LMHs exclusion, whether by natural processes or experimental

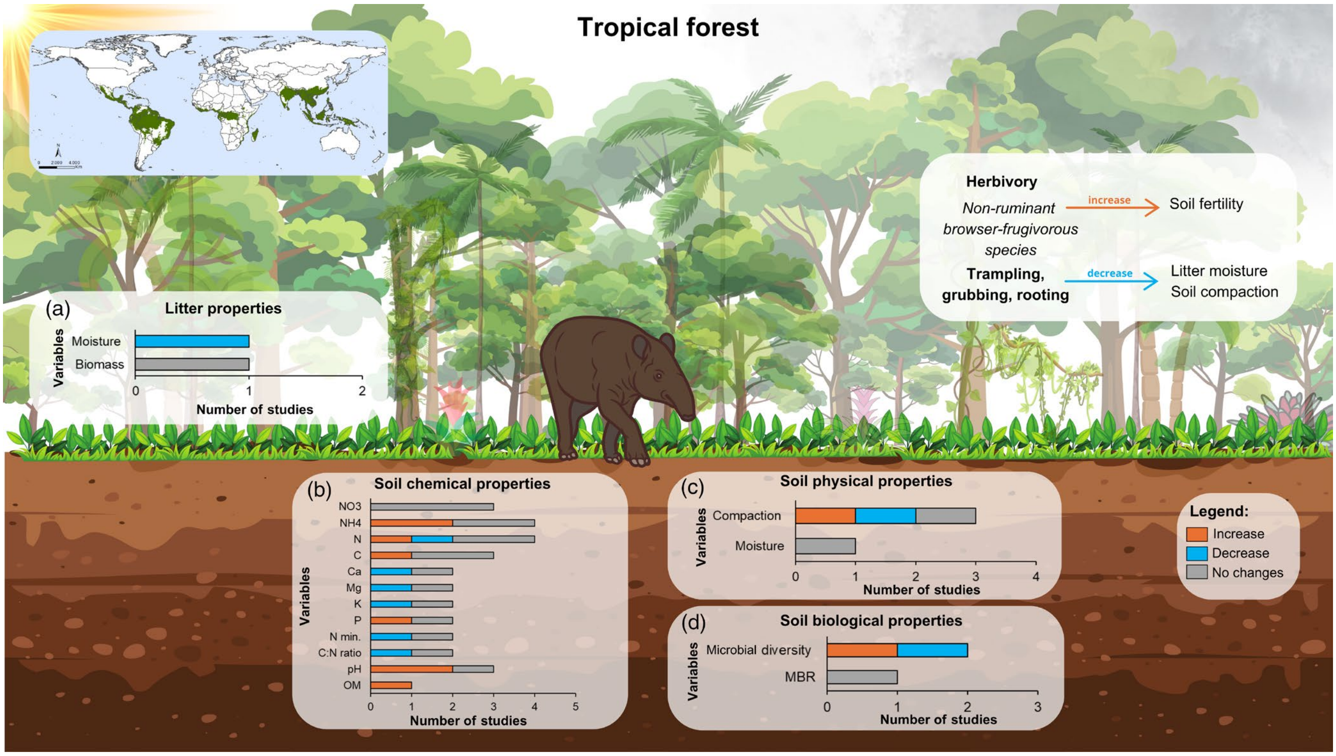

FIGURE 6 Effect of ground-dwelling large mammalian herbivores (LMHs), principally wild boar (*Sus scrofa*), peccaries (*Tayassu pecari* and *Dicotyles tajacu*) and lowland tapir (*Tapirus terrestris*) on litter (a), soil chemical (b), physical (c) and biological (d) properties in tropical forests. MBR, microbial basal respiration; OM, organic matter. Orange indicate an increase, blue a decrease, and grey effects indicate no change in the measured variable in the presence of LMHs. Created with CanvaPro.

exclusion (Forbes et al., 2019). Reported durations of exclusion in reviewed studies range from 1 month to 70 years (Appendix S2). In addition, some studies monitored experiments over multiple years, comparing results over time, while others were based on a single sampling event (Ellis & Leroux, 2016; Kumbasli et al., 2010; Risch et al., 2010). For example, after 7 years of invasive red deer exclusion in a temperate forest, Relva et al. (2014) observed no changes in litter or soil properties, despite significant changes in understorey vegetation. In contrast, Furusawa et al. (2005) reported changes in soil chemical properties after only 3 years of red deer exclusion. However, even after 60 years of wild boar exclusion, Bruinderink and Hazebroek (1996) found no effects on soil chemical or physical properties in a temperate forest. These results suggest that the effects of LMHs on belowground conditions depend on a combination of abiotic and biotic factors, including the duration of exclusion experiments, frequency of data collection and such variability may help explain the lack of consistent patterns across studies (Maillard et al., 2021).

3.3.4 | Geographical bias

Most studies investigating the effects of LMHs on litter and soil properties have been conducted in temperate forests of the Northern Hemisphere. Most of these studies were experimental exclusion plots conducted in the United States, Japan and Europe. Temperate and boreal forests cover a larger area of the globe than tropical forests (Bouwman, 1990; Burton et al., 2003), so it is understandable that they have been studied more extensively. Moreover, temperate forests are predominantly located in economically developed and scientifically advanced regions, whereas tropical forests are primarily found in developing or underdeveloped countries (Minasny et al., 2020). In addition, our limited understanding of tropical forests may be also due to the diversity of these systems (Cavaleri et al., 2015). Tropical forests exhibit a wide range of mean annual temperatures, seasonality, precipitation (Richards, 1952), edaphic conditions (Townsend et al., 2008) and fauna and flora diversity (Leigh et al., 2004). These diverse and complex ecosystems create confounding factors that can complicate studies of interactions between biotic and abiotic components. In addition, the high cost of establishing and maintaining exclusion experiments in such highly weathered conditions can reduce the lifespan of experiments and require substantial long-term funding (Berzaghi et al., 2018).

4 | FUTURE DIRECTIONS

LMHs are one of the main groups threatened by defaunation and the loss of these species can lead to profound changes in ecosystem dynamics, highlighting the urgent need to fill critical knowledge gaps in this area (Brodie et al., 2024; Dirzo et al., 2014).

Specifically, studies on the effects of LMHs on belowground processes in the Global South remain limited. More long-term studies are needed in tropical forests, especially in Africa, India, Southeast Asia and Central and South America where there is still a great diversity of herbivorous mammals and where the effects of these LMHs on below-ground are still poorly known (Ahrestani & Sankaran, 2016; Gallina-Tessaro, 2019; Kingdon, 2014; Pringle et al., 2023).

Current research has focused primarily on folivorous LMHs, especially browsers and mixed feeders, while ground-dwelling frugivorous species are largely overlooked. Frugivory introduces distinct ecological mechanisms, such as the deposition of nutrient-rich fruits and species-specific foraging behaviours, which may influence soil processes and plant–soil feedback (Sridhara et al., 2016; Villar et al., 2020). Future studies should therefore explicitly consider the functional diversity of LMHs, including the role of frugivores, to better understand how different feeding strategies shape belowground dynamics.

Beyond the traditional focus on physical and chemical soil properties, we emphasize the need for a more integrated approach that includes biological components of the soil, such as microbial communities and soil fauna. This perspective is critical for uncovering how herbivore-driven changes propagate through the soil food web and ultimately affect nutrient cycling (Tomita et al., 2025).

Another important question for future research is the role of LMHs in regulating carbon stocks through their effects on belowground processes and the potential implications for climate mitigation (Kristensen et al., 2022; Malhi et al., 2022; Tanentzap & Coomes, 2011). When decelerating nutrient cycling in forest ecosystems, LMHs may promote more stable soil carbon stocks, potentially through the production of recalcitrant litter that decomposes slowly (Prescott & Vesterdal, 2021; Wardle et al., 2004). However, these effects are likely context dependent. As observed for other soil properties, LMH impacts on soil carbon vary with species composition and forest type, and similar variability can be expected for soil carbon stocks. This highlights the urgency for empirical studies examining these relationships. Such studies are essential for evaluating the potential contributions of LMHs to climate mitigation, as these animals may influence greenhouse gas fluxes both directly and indirectly through their effects on soil nutrient cycling (Cromsigt et al., 2018; Malhi et al., 2022).

Understanding the effects of LMHs on litter and soil properties, and consequently on nutrient cycling, is not only essential for advancing basic ecological knowledge; it also has significant implications for predicting how climate change may disrupt these interactions and for exploring how LMHs could potentially enhance ecosystem resistance and resilience (Malhi et al., 2022; Sandom et al., 2020). For example, knowing the role of LMHs on belowground properties can help predict the effects of trophic rewilding on nutrient cycling, or even improve species selection based on the ecosystem process to be restored (Schmitz et al., 2023).

5 | CONCLUSION

1. Research on the effects of LMHs on litter and soil properties has predominantly focused on temperate and boreal forests, with few studies in tropical forests, despite a greater diversity of LMHs.
2. In the reviewed studies, wild boar (non-ruminant browsers) and cervids (ruminant browsers) are the main LMHs species with native and invasive distributions. Wild boar is generally associated with positive effects on belowground properties and cervids with negative effects.
3. There are several reports of null results of the effect of LMHs, showing a complexity of isolating the effect of LMHs from confounding factors, since belowground properties are strongly influenced by abiotic factors.
4. While LMHs are hypothesized to reduce nutrient cycling in forest ecosystems, this effect appears to be highly context-dependent (varying with site location, season, sampling period and exclusion time), underscoring the need for further research, especially in tropical forests.

AUTHOR CONTRIBUTIONS

Letícia Gonçalves Ribeiro, Mateus Melo-Dias and Beatriz Maria Paccas Saraiva collected the data. Beatriz Maria Paccas Saraiva and Mateus Melo-Dias developed map figures. Letícia Gonçalves Ribeiro, Mateus Melo-Dias, Nacho Villar and Mauro Galetti were involved in data analysis, conceptualization and writing. All authors contributed to revising the manuscript and approved the submitted version.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data are available from the Zenodo public repository: https://doi.org/10.5281/zenodo.17130907 (Ribeiro et al., 2025).

ORCID

Letícia Gonçalves Ribeiro https://orcid.org/0000-0002-1059-1516
Nacho Villar https://orcid.org/0000-0003-3609-4080

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1.

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