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REVIEW

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Synthesizing the effects of large, wild herbivore exclusion on ecosystem function

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Abstract

1. Wild large herbivores are declining worldwide. Despite extensive use of exclosure experiments to investigate herbivore impacts, there is little consensus on the effects of wild large herbivores on ecosystem function.
2. Of the ecosystem functions likely impacted, we reviewed the five most-studied in exclosure experiments: ecosystem resilience/resistance to disturbance, nutrient cycling, carbon cycling, plant regeneration, and primary productivity.
3. Experimental data on large wild herbivores' effects on ecosystem functions were predominately derived from temperate grasslands (50% grasslands, 75% temperate zones). Additionally, data were from experiments that may not be of adequate size (median size 400 m^2 despite excluding all experiments below 25 m^2) or duration (median duration 6 years) to capture ecosystem-scale responses to these low-density and wide-ranging taxa.
4. Wild herbivore removal frequently impacted ecosystem functions; for example, net carbon uptake increased by three times in some instances. However, the magnitude and direction of effects, even within a single function, were highly variable.
5. A focus on carbon cycling highlighted challenges in interpreting effects on a single function. While the effect of large herbivore exclusion on carbon cycling was slightly positive when its components (e.g. pools vs. fluxes of carbon) were aggregated, effects on individual components were variable and sometimes opposed.
6. Given modern declines in large wild herbivores, it is critical to understand their effects on ecosystem function. However, this synthesis highlights strong variability in direction, magnitude, and modifiers of these effects. Some variation is likely due to disparity in what components are used to describe a given function. For example, for the carbon cycle we identified eight distinctly meaningful components, which are not easily combined yet are potentially misrepresentative of the larger cycle when considered alone. However, much of the observed difference in responses likely reflects real ecological variability across complex systems.
7. To move towards a general predictive framework we must identify where variation in effect is due to methodological differences and where due to ecosystem context. Two critical steps forward are (a) additional quantitative synthetic

analyses of large herbivores' effects on individual functions, and (b) improved, increased systematic exclosure research focusing on effects of large herbivores' exclusion on functions.

KEYWORDS

carbon cycle, ecosystem function, ecosystem resilience and resistance, exclosure experiment, large herbivore loss, nutrient cycling, plant regeneration, primary productivity

1 | INTRODUCTION

Large-bodied wildlife are declining precipitously in distribution and abundance (Ceballos et al., 2015; Young, McCauley, Galetti, & Dirzo, 2016), especially taxa of large mammalian herbivores (Smith, Smith, Lyons, & Payne, 2018). The loss of these herbivores not only constitutes a critical loss of intrinsic biodiversity but is hypothesized to have broad impacts on ecosystem functions. However, quantitative syntheses of the impacts of biodiversity loss on ecosystem functions have focused nearly exclusively on studies of small or sessile organisms like invertebrates and plants (Delgado-Baquerizo et al., 2015; Hooper et al., 2012; Soliveres et al., 2016). The lack of synthesis is surprising given that (a) large taxa are often suggested to have disproportionately influential roles on ecosystem function (Owen-Smith, 1988; Pringle, Palmer, Goheen, McCauley, & Keesing, 2010) (Figure 1), and (b) multiple efforts have attempted to synthesize effects of excluding large, wild herbivores on producers (e.g. Gruner et al., 2008, Jia et al., 2018) and smaller consumers (Daskin & Pringle, 2016; Foster, Barton, & Lindenmayer, 2014).

Yet, there is a rich body of theoretical and empirical literature on the effects of large wild herbivores (>5 kg; hereafter large herbivores) on ecosystem functions stretching back decades (e.g. McNaughton, 1979). These species often fill functionally unique roles in ecosystems. For instance, their large body size allows for very high plant consumption (Clauss, Steuer, Müller, Codron, & Hummel, 2013), large geographic ranges of movement, long-distance transport of nutrients via their waste (Wolf, Doughty, & Malhi, 2013), and unique capability to physically modify habitats via soil compaction and cracking, erosion, and by breaking woody vegetation (Beck, Thebpanya, & Filiaggi, 2010; Long, Wambua, Goheen, Palmer, & Pringle, 2017; Pringle, 2008; van Klink, van der Plas, van Noordwijk, WallisDeVries, & Olff, 2015). The effects of large herbivores on both producers and consumers are often, but not always (see Jia et al., 2018 and Koerner et al., 2018) mediated by environmental variables, for example ecosystem productivity (Burkepile et al., 2017; Daskin & Pringle, 2016), which may mediate herbivore effects on several ecosystem functions (Figure 1).

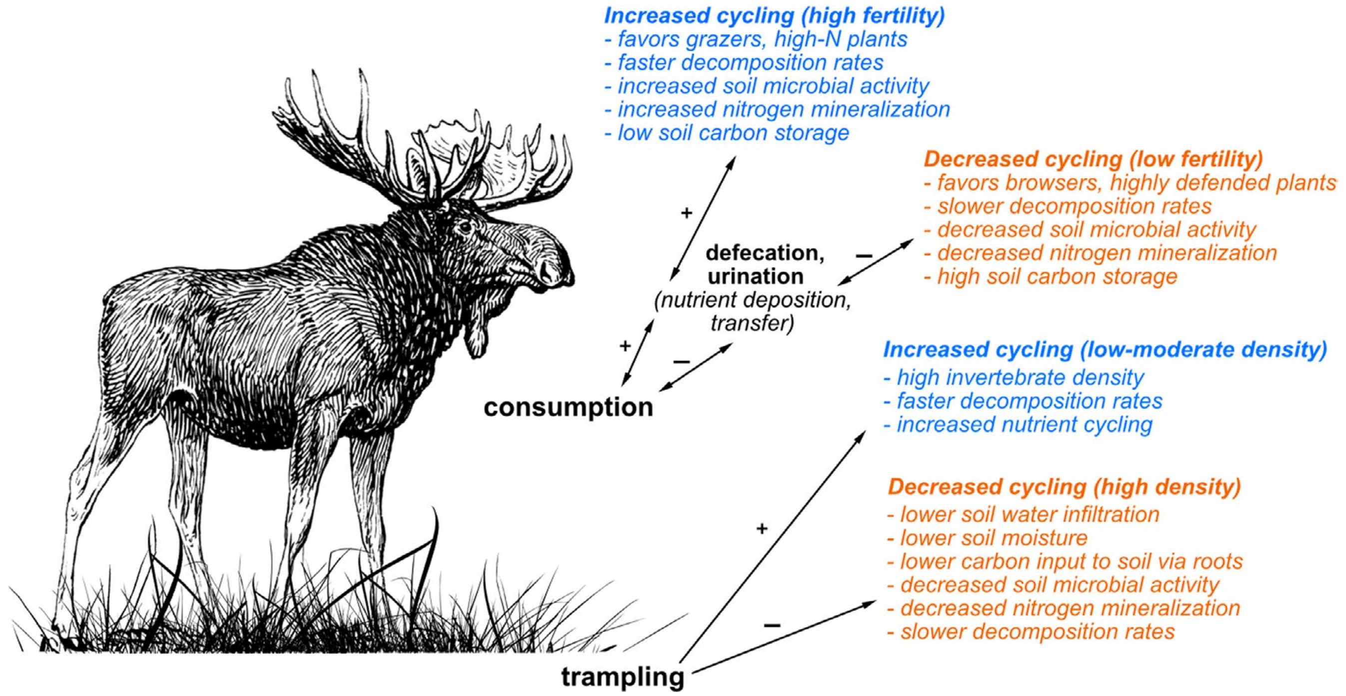

FIGURE 1 Hypothesized influences of large herbivores on an example ecosystem function: nutrient cycling. Direct effects of large herbivores (consumption, trampling) lead to highly context-dependent (ex: herbivore density, ecosystem fertility) indirect outcomes on nutrient cycling. Orange text denotes decelerating effects on nutrient cycling; blue denotes accelerating

Here, we review the impacts of experimental removal of large herbivores on five commonly-studied ecosystem functions: ecosystem resilience/resistance, nutrient cycling, carbon cycling, plant regeneration, and primary productivity. Though distinct, these functions are often linked or synergistic (e.g. nutrient cycling influencing carbon cycling) (Bennett, Peterson, & Gordon, 2009). We focus this review exclusively on terrestrial exclosure experiments involving large wild herbivores, though we briefly discuss aquatic and domestic herbivores when discussing the importance of ecological context. We also present a meta-analysis on how large herbivores affect carbon cycling, which highlights different responses among the components of a single function.

2 | EXCLOSURE EXPERIMENTS: DISTRIBUTION AND BIASES

We identified 17 candidate ecosystem functions likely impacted by large herbivores (Appendix S1) and used standardized search procedures to identify 174 unique published experiments that (a) excluded large, native, wild herbivores from plots at least 25 m^2 (to better capture indirect effects, and reduce likelihood of edge effects swamping treatment effects), and (b) collected data on ecosystem functional responses (Appendix S2, Table S1). While restricting this search to exclosure experiments has limitations (e.g. experimental artifacts, practical limits to size and duration of experiments; Diamond, 1983), these manipulations provide a controlled method to isolate the impacts of total removal of large herbivores on ecosystem function (Bakker et al., 2015). While natural experiments (e.g. observations of widespread herbivore loss or decline) are integral in detecting large-scale, long-term impacts of environmental perturbation on ecosystem functions like ecosystem resilience and resistance (Caves, Jennings, HilleRisLambers, Tewksbury, & Rogers, 2013), they are difficult to replicate and often have confounding covariates (e.g. impacted sites often experience multiple human uses, climate change may confound temporal comparisons). Natural experiments also display more nuanced variation in herbivore density (e.g. decline rather than total removal), making comparisons between them more difficult.

Plot sizes in exclosure experiments in our synthesis ranged from 25 m^2 to 128 km^2 (median size 400 m^2; Appendix S2). Duration of exclosure ranged from <1 year to 85 years (median 6 years). We found 12 of the 17 a priori identified functions had been explicitly studied with exclosure experiments, totaling 107 unique publications and 288 individual functional responses from 174 unique experimental sites (Figure 2). The great majority (86%) of functional responses to large herbivore exclusion experiments concentrated on just five functions: (a) ecosystem resistance/resilience, (b) nutrient cycling, (c) carbon cycling, (d) plant regeneration, and (e) primary productivity, and we limited our review to these (Figure 3a,b). Research was heavily concentrated in temperate biomes (approximately 75%; Figures 2 and 4) and grasslands (approximately 51%; Figure 5) (Appendix S2), despite evidence that size-selective defaunation is most pervasive in the tropics (Fritz, Bininda-Edmonds, & Purvis, 2009).

3 | INSIGHTS FROM WELL-STUDIED ECOSYSTEM FUNCTIONS

3.1 | Nutrient cycling and translocation

Large herbivores often cause strong changes in nutrient cycling, although the magnitude and even direction of effect is typically understood to vary across contexts. Generally, large herbivores are thought to accelerate nutrient cycling in highly productive ecosystems with long histories of herbivory, and with low to moderate grazing intensities (de Mazancourt, Loreau, & Abbadie, 1998; McNaughton, Banyikwa, & McNaughton, 1997). Although there are many pathways involved, the main mechanism is via the conversion of large quantities of aboveground biomass into labile waste products (Tracy and Frank 1998). Large herbivores also shift plant

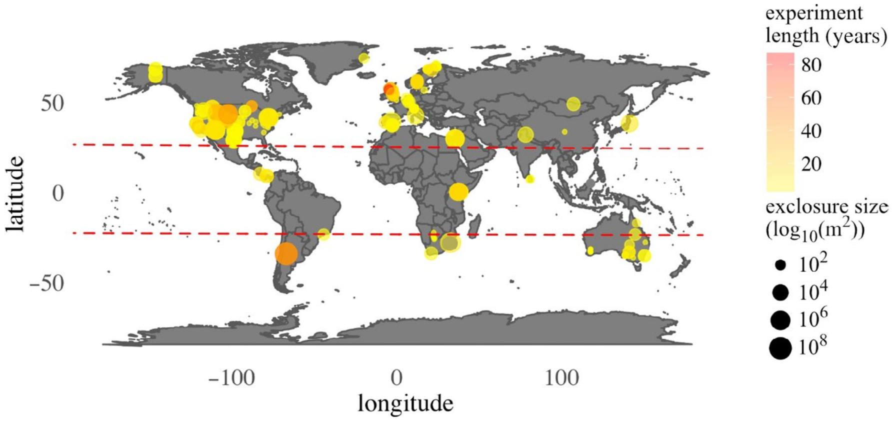

FIGURE 2 Map of 117 distinct, published functional responses to large herbivore removal with experimental exclosures. Point color (yellow-red) indicates duration of exclosure experiment at time response data were collected; point size indicates exclosure size. Note a single exclosure site could have multiple responses published from it (e.g. more than one function measured; a single function measured at experimentally distinct times, or in ecologically distinct locations within the experiment). Points with high opacity thus indicate a site from which multiple responses were published, opacity increasing with the number of unique responses

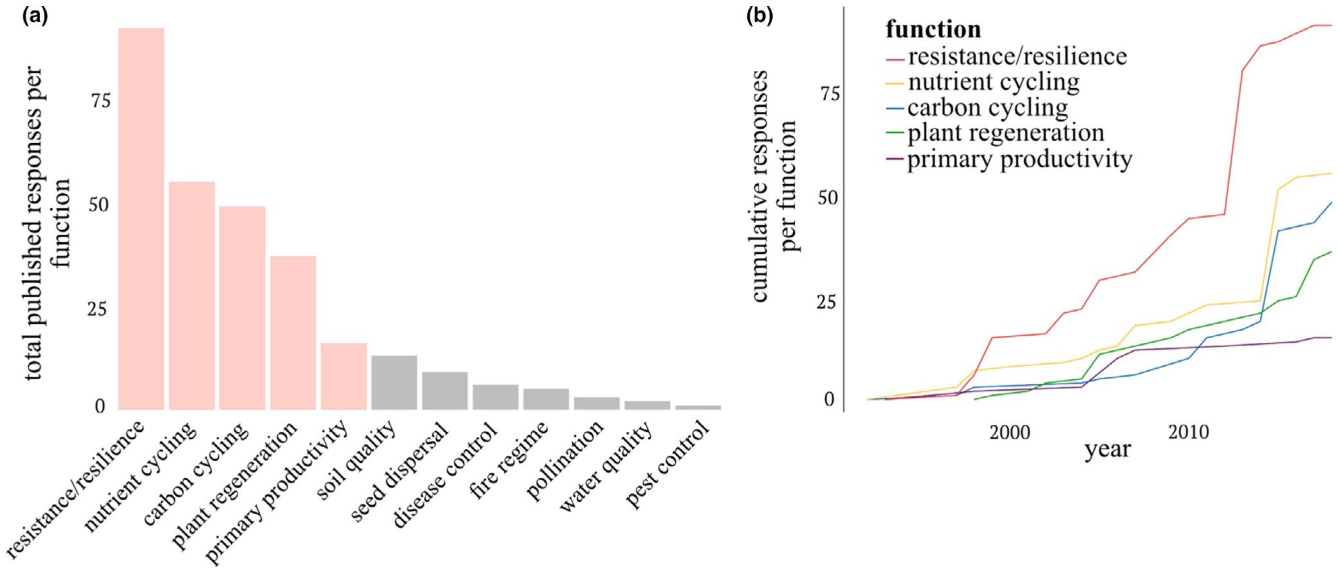

FIGURE 3 (a) Total number of published responses per function. The top 5 most commonly-studied functions under these parameters, marked in red, comprise 87% of published efforts and are the focus of this review. (b) Cumulative number of functional responses of the five most- studied ecosystem functions, over time, demonstrating trends in the academic study of ecosystem functional response to experimental large herbivore loss

allocation of nutrients to roots, increasing soil microbial activity and in turn soil nitrogen mineralization (Ruess & McNaughton, 1987). In contrast, large herbivores in low-productivity systems or those with historically low population densities often decelerate nutrient cycling (Bardgett & Wardle, 2003) via selective foraging for nutrient-rich plants, which subsequently shifts communities toward species that decompose slowly (e.g. Harrison & Bardgett, 2004).

However, in contrast to this general theory, many studies have found contradictory effects. In some cases, increased productivity simply does not result in accelerated nutrient cycling (e.g. Cherif & Loreau, 2013, Stark, Männistö, & Eskelinen, 2015). In other cases, effects are more associated with location- and time-specific variation (e.g. Wardle, 2002, Stark, Strömmer, & Tuomi, 2002); for example, summer grazing by reindeer increases tundra nutrient cycling rates from fecal nutrient deposition, while winter grazing results in the opposite when these nutrients leach from the system (Stark & Grellman, 2002; Stark, Julkunen-Tiitto, & Kumpula, 2007). This inconsistency in effect may be because secondary mechanisms (soil compaction, temperature, trampling, litter chemistry, lateral nutrient transport, among others) override the general mechanisms detailed above. Unfortunately, there is currently no theory to integrate these highly disparate results into a predictive framework. This gap has prompted a call to revisit the generalizations about productivity mediating herbivore effects on nutrient cycling and conduct more rigorous synthesis to help identify other moderators (Sitters & Venerink, 2015).

An important caveat in interpreting these results is that work from exclosure experiments is, logistically, almost exclusively focused on nutrient cycling within a system, ignoring lateral transfer of nutrients between systems or across space within a system. However, the important effects of lateral nutrient transfer are well documented and may often overpower the effects of herbivory on nutrient cycling within systems (e.g. Leroux & Schmitz, 2015; Stark et al., 2015). Moose and hippopotamus, for example, move substantial quantities of nutrients between terrestrial and aquatic ecosystems, increasing nutrient availability and subsidizing consumers in recipient systems (Stears et al., 2018); similarly, rhinoceroses maintain nutrient (and secondarily, structural) heterogeneity via the lateral transfer of nutrients across a single savanna system (Veldhuis, Gommers, Olff, & Berg, 2017). Though exclosure experiments are generally inappropriate to study these landscape-scale effects of herbivores on nutrient cycling, recent synthesis nonetheless suggests that effects of such transfer likely vary across characteristics of both nutrient donor and recipient ecosystems and the herbivore species involved (Subalusky & Post, 2019).

3.2 | Ecosystem resilience and resistance

Resilience is often defined as an ecosystem's capacity to return toward its previous state following a disturbance, while resistance generally refers to an ecosystem's ability to maintain its integrity in the face of that disturbance (Mitchell, Auld, Duc, & Marrs, 2000). Exclosure experiments have addressed the resilience/resistance of microbial community dynamics (Hodel et al., 2014; Rudgers et al., 2016), exotic species invasions (Ender, Christian, & Cushman, 2017; Seabloom, Borer, Martin, & Orrock, 2009), nutrient dynamics (Bakker, Knops, Milchunas, Ritchie, & Olff, 2009), and chemical or physical defense (Young, Stanton, & Christian, 2003). For example, removal of large herbivores often results in dramatic reductions in plant defenses, making them less resistant to future herbivory (Palmer et al., 2008; Ward & Young, 2002; Young & Okello, 1998). Large herbivore exclusion can also lead

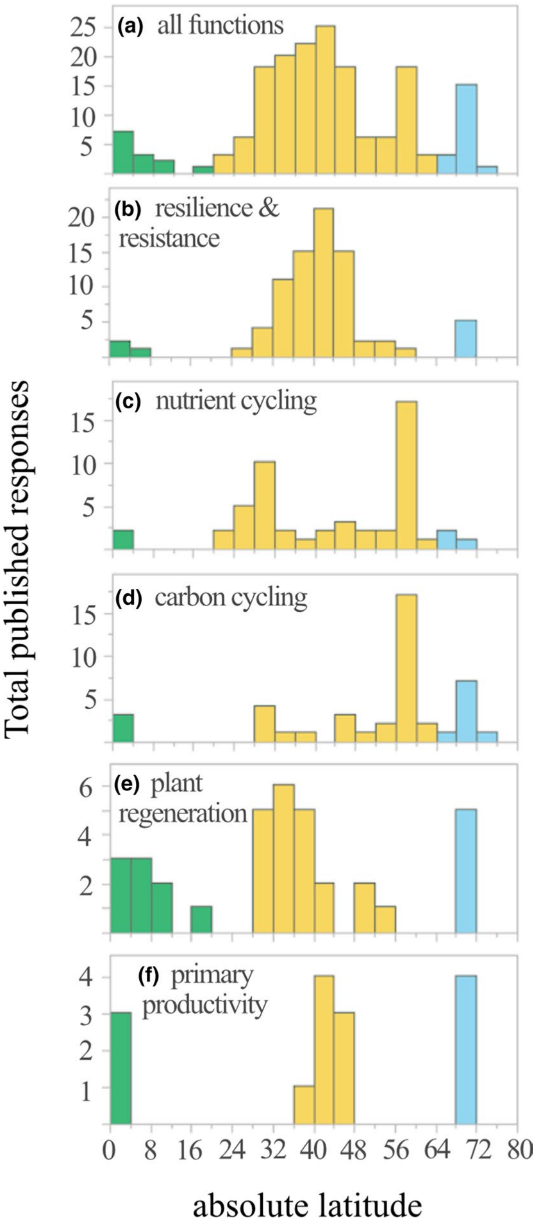

FIGURE 4 Total number of responses to large herbivore exclosure, arranged by absolute latitude, with green indicating that data are from the tropics, yellow from temperate zones, and blue from the arctic, together and separately for each of the five functions reviewed: (a) all functions, (b) resilience/resistance, (c) nutrient cycling, (d) carbon cycling, (e) plant regeneration, and (f) primary productivity

to increases in exotic plants (Ender et al., 2017; Seabloom et al., 2009) suggesting that wild herbivores help ecosystems resist exotic plant invasions.

The concept of resilience/resistance may be best captured by how herbivores impact plant communities or ecosystem processes after a disturbance such as fire or drought (Porensky, Wittman, Riginos, & Young, 2013). Unfortunately, due to the experimental difficulty, exclosure experiments are not often combined with other disturbances or conducted on temporal scales long enough to test questions of resilience or resistance. However, observational data combined with what experimental data do exist suggest that herbivores and fire act synergistically to influence resilience and resistance of plant communities, especially the transition between grass- and woody-dominated communities. In African savannas, fire and large herbivores together suppress woody vegetation growth and facilitate grasses (Augustine & McNaughton, 2004; Staver, Bond, Stock, Rensburg, & Waldram, 2009). Large herbivores also keep woody individuals small, and more likely to be killed by fire (Midgley, Lawes, & Chamaillé-Jammes, 2010). Both mechanisms suggest a strong link between large herbivores and savanna resilience. Indeed, large herbivore removal allows woody plants to grow tall enough to resist the effects of fire (Staver & Bond, 2014). Elephants, the largest herbivores, may be one of the only forces that can facilitate the resilience of grass-dominated ecosystems *after* woody plants establish (Dublin, Sinclair, & McGlade, 1990; Pringle et al., 2015; Skarpe et al., 2004).

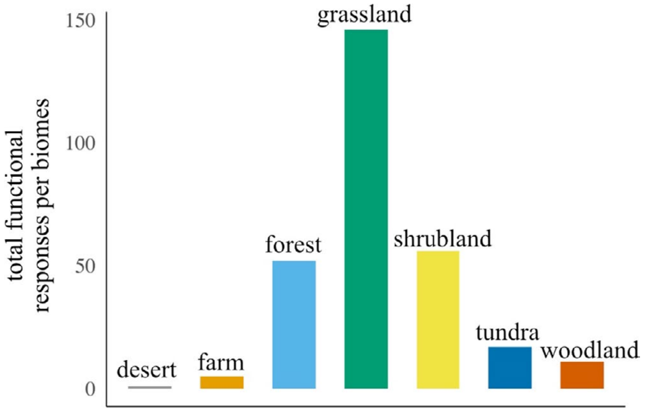

FIGURE 5 Total number of responses to large herbivore exclosure, by biome. Biomes provided in publications were binned into broad categories (e.g. savanna, prairie in "grassland") to demonstrate general patterns in the locations of studies examining large herbivore exclosure on ecosystem function

In mesic grasslands of North America, fire frequency appears to be the primary driver of ecosystem resistance, with frequent fires suppressing establishment of woody vegetation (Briggs et al., 2005). Therefore bison (and non-wild livestock) may in fact hasten woody vegetation expansion, as grazing removes fuel loads and subsequently lowers fire intensity and grass competition. However, these dynamics were only captured with decades-long fire manipulations. Thus, addressing how herbivores affect resilience/resistance to disturbances will be more difficult to capture at the temporal scales of most experiments (Figure 6).

3.3 | Plant regeneration

Large herbivores can strongly impact many components of plant regeneration (germination, recruitment, survival, etc.; Kurten, 2013) through a wide range of mechanisms, ranging from direct consumption to indirect effects of competition or facilitation. They can increase seed germination and emergence, for example by

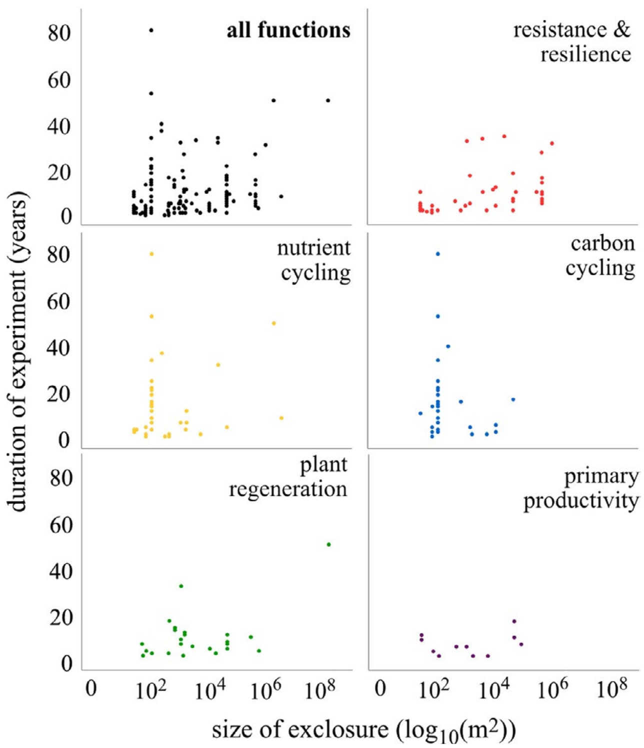

FIGURE 6 Distribution of elapsed duration and size of physical exclosures used to measure the responses of the top-five most studied ecosystem functions in the literature. The clustered spread of these experiments, both in total and separated by function, indicates both a size and time bias in these data: data frequently come from smaller and shorter-duration exclosure sites upon publication. Separated by function, these trends are generally retained with some variation across functions

suppressing small consumers that prey on seeds (Goheen, Palmer, Keesing, Riginos, & Young, 2010; Maclean, Goheen, Doak, Palmer, & Young, 2011). However, dispersal-dependent components like seedling community composition (Kurten, Wright, & Carson, 2015) and seedling diversity (Granados, Bernard, & Brodie, 2018) vary due to differences in predominant dispersal method in a given ecosystem (biotic or abiotic). As with other functions, effects on plant regeneration are often contextually dependent on the identity and ecology of the herbivores in question. For instance, herbivores selectively consuming palatable species suppress their regeneration, favoring dominance of unpalatable species. However, if the herbivores are migratory, seasonally-intense herbivory may favor regrowth of palatable species and result in their dominance (Augustine & McNaughton, 1998). Herbivore body size also influences plant regeneration; very large herbivores (elephant, wildebeest) and smaller large herbivores (impala, warthog) can have equally-strong, but sometimes contrasting effects on plant species dominance, productivity, and seedling survival, and thus on community richness (Burkepile et al., 2017). Notably, herbivore density, migration patterns (Augustine & McNaughton, 1998), and range size (Granados et al., 2018) can cause effects on plant regeneration to be spatially and temporally irregular.

Effects of large herbivores on plant regeneration also vary at different plant life stages. For example, when large herbivores are excluded, flowering and fruiting success can increase dramatically as these parts are no longer consumed (Pringle et al., 2014; Wilkerson, Roche, & Young, 2013; Young & Augustine, 2007). However, as previously mentioned, when small mammal populations increase in large mammal exclosures due to competitive release, they can cause significant increases in seed and seedling predation (Goheen, Keesing, Allan, Ogada, & Ostfeld, 2004; Goheen et al., 2010; MacLean et al., 2011). The net effect of these opposing forces depends in part on the size and functional role of the large herbivores involved.

For example, excluding only elephants in a Kenyan savanna had weak positive effects on community-level shrub density, despite their strong negative effects on adult shrub survivorship and reproduction. One possible explanation is that in the absence of elephants, rodents' increased seed predation led to less shrub recruitment. However, when other large herbivores were also excluded, shrub density increased dramatically, despite even greater rodent seed predation, apparently due to increased fruit production and reproductive output of shrubs in the absence of those herbivores who specifically impact the fruits, and thus reproductive output, of mature plants (Pringle et al., 2014). Another example of potentially-opposing effects is preferential browsing of palatable species by large herbivores, which can decrease regeneration via direct consumption of plant material, but also increase it via mechanisms like increased nutrient input or beneficial migration-based herbivory regimes (Augustine & McNaughton, 1998). Once again, the observed variability in responses is likely driven by variation in ecosystem properties like soil fertility (Olff & Ritchie, 1998) and ecosystem productivity (Burkepile et al., 2017).

3.4 | Primary productivity

The activity of large herbivores (as consumers, disturbance agents, and fertilizers) can serve as major drivers of primary productivity (Bardgett & Wardle, 2003; Milchunas & Lauenroth, 1993). Although most exclosure research has focused on grass- and grass/shrub-dominated landscapes, even within this context effects are extremely variable: the effects of herbivores on primary productivity can vary from positive (e.g. McNaughton, 1983, Charles, Porensky, Riginos, Veblen, & Young, 2017) to negative (e.g. Pastor, Dewey, Naiman, McInnes, & Cohen, 1993, Ritchie, Tilman, & Knops, 1998), depending on the ecosystem in question. As with nutrient cycling, large herbivores broadly promote primary productivity when soil nutrients and moisture are abundant, grazing intensity is light to intermediate, and herbivores and plants share long evolutionary histories. In contrast, they often have neutral or negative effects when soil resources are low, grazing intensities are high, and evolutionary histories between herbivores and plants are short (Milchunas & Lauenroth, 1993).

While most studies have addressed the effects of herbivores on aboveground productivity, focus has increasingly expanded to include belowground productivity. Large herbivores can have positive (Frank, Kuns, & Guido, 2002), neutral (McNaughton et al., 1997) or negative effects (Archer & Tieszen, 1983) on belowground productivity. In some cases, herbivores drive above- and belowground productivity in the same direction, while opposing effects occur in other systems. For example, grazers in northern India increase aboveground primary productivity but reduce it belowground (Bagchi & Ritchie, 2010), while in Yellowstone National Park ungulates stimulate increases in both above and belowground productivity (Frank et al., 2002). As with other functions, analysis incorporating both systematic context (e.g. soil and vegetation community properties, number and type of large herbivores) and the components of the function that were measured (e.g. above or belowground productivity) is crucial to understand observed variation.

Despite obvious differences among herbivore types, and potential for interactions among these species, effects of herbivore identity and composition on primary productivity have received relatively little attention. A noteworthy exception is the work of Charles et al. (2017), who addressed the individual, additive and interactive effects of co-occurring wild herbivores (and livestock) on ecosystem function with large-scale, size-selective exclosures. In this system, aboveground primary productivity did not differ between plots with both large herbivores and mega-herbivores (giraffe and elephants) and plots with only large herbivores. However, the addition of domestic cattle to the large herbivores-only communities enhanced aboveground primary productivity, though this effect was reduced when mega-herbivores were also present. Typical herbivore exclusion experiments may not pick up these nuanced effects as they rarely address the different functional roles of herbivores.

3.5 | Carbon cycling: a case study

As noted for other functions, the effects of large herbivores on carbon cycling varies enormously across systems. This variation is hypothesized to be driven both by ecosystem properties like productivity (Piñeiro, Paruelo, Oesterheld, & Jobbágy, 2010), grazing intensity (Olofsson, Kitti, Rautiainen, Stark, & Oksanen, 2001), and spatial heterogeneity (Vowles, Lovehav, Molau, & Bjork, 2017), as well as experimental properties like plot size and duration (Marburg et al., 2013). Yet much of the observed variability is likely also due to the challenges associated with measuring a function. What is often putatively considered a single function (e.g. carbon cycling) often truly consists of multiple, loosely related, sometimes even opposing components (e.g. measurements of carbon fluxes vs. pools). Variability in selection of components to measure a given function can result in an inability to generalize results across systems (Dale & Beyeler, 2001). To better understand the sources of variability in responses, we conducted a quantitative analysis for carbon cycling, an important function for which management is of high interest due to climate change, and for which recent study has made apparent the consequential role of large herbivores (Schmitz et al., 2014).

The carbon cycle is an integrated system that refers to both pools (storage) and fluxes (cycling between pools) of carbon. Large herbivores directly impact carbon pools and fluxes through plant consumption, trampling plants and soil, removing woody vegetation like trees, and depositing waste products (Asner & Levick, 2012; Heggenes et al., 2017; Tanentzap & Coomes, 2012). Large herbivores also impact carbon storage and flux indirectly. For example, plants under moderate herbivory may reallocate carbon belowground to their roots, increasing belowground carbon storage despite aboveground biomass decreasing (Ritchie et al., 1998). Reindeer exclusion in the Arctic can decrease soil carbon dioxide flux (lessening emissions to the atmosphere) because of lower soil temperatures, while weakening soil's impacts as a methane sink (another, more potent carbon-based greenhouse gas) due to increased coverage of methane-producing lichens and bryophytes (Cahoon, Sullivan, Post, & Welker, 2012; Köster, Köster, Berninger, Heinonsalo, & Pumpanen, 2017). While all effects of large herbivores should be considered effects on carbon cycling, individual components should neither be conflated nor considered representative of the cycle on their own.

To better understand the effects of herbivores on the carbon cycle, and the extent to which component selection risks conflating incomparable effects, we conducted a meta-analysis (detailed in Appendix S2). We began by considering the entire suite of components that describe the carbon cycle, identifying 121 individual responses to large herbivore exclusion that represented an aspect of the carbon cycle. Overall, we revealed a slightly positive net effect of large herbivore exclusion on the “carbon cycle” when all components were pooled (Figure 7a). However, as discussed above, this result should be interpreted thoughtfully as it aggregates the multiple, inherently correlated components (both pools and fluxes) of the carbon cycle (Falkowski et al., 2000).

Therefore, stronger and more mechanistically meaningful responses would be expected for individual components. We identified eight components of carbon cycling reflected by the group of 121 responses and binned each response into one. Several of these components contained multiple, correlated metrics with which they were measured in the field (e.g. methane *and* carbon dioxide flux binned within carbon flux). Analyzing these distinct components revealed that some showed clear directionality while others remained highly variable. This is important, as the differences in response between components underscores how dissimilarities in study focus (e.g. which component is being measured) within a single function can precipitate different interpretations of the effects of large herbivore exclusion. For example, while carbon stored in soil increases in response to large herbivore exclusion (Figure 7c), the response of soil carbon flux is highly variable and trends negative (Figure 7b). Interpreting these contrasting results requires attention to what effect direction means for each component: herbivore exclusion seems to *increase* carbon storage significantly but can *decrease or increase* carbon emissions. Assessing the impacts of large herbivore exclusion on one component to represent the carbon cycle writ large may therefore result in management recommendations of limited value. For example, large herbivore exclusion results in higher aboveground biomass globally, a critically important pool of carbon. However, suggesting large herbivore removal to increase carbon

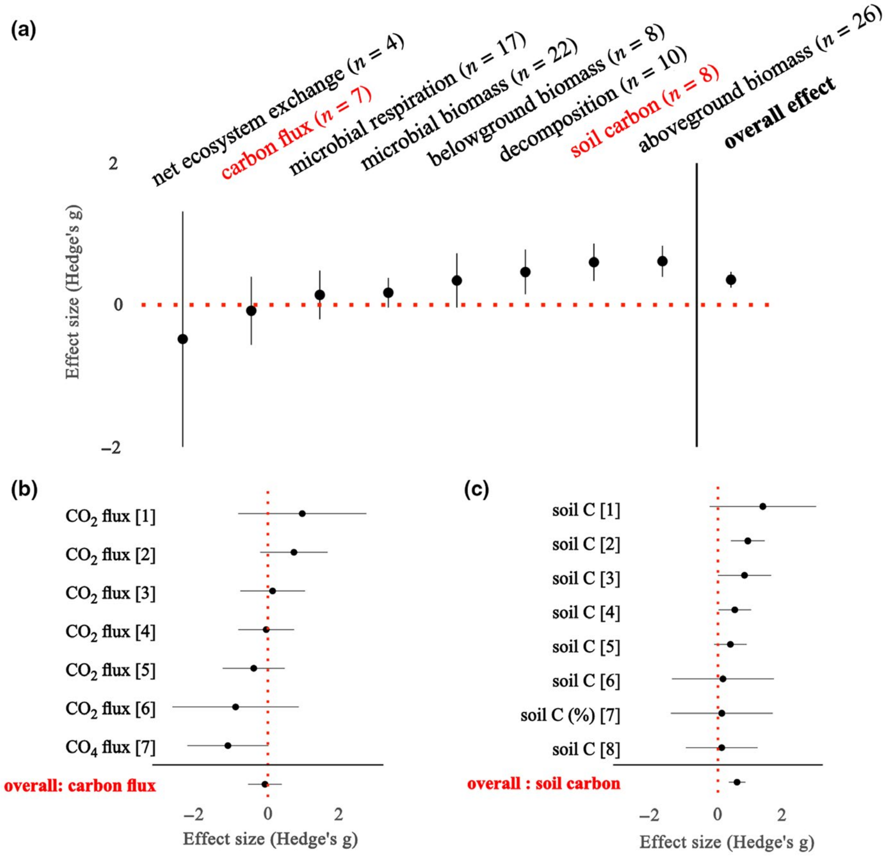

FIGURE 7 (a) Average effect size (Hedge's G) and 95% confidence intervals of large herbivore exclusion on eight metrics of ecosystem carbon cycling; effects of large herbivore exclusion are not consistent across metrics. (b, c) illustrate further variability within-metric, with forest plots of collected published data on responses of carbon flux and soil carbon (respectively) demonstrating variation in magnitude and direction of effect. Numbers next to labels in (b) and (c) reference experimentally unique responses to large herbivore exclusion

sequestration (Tanentzap & Coomes, 2012) overlooks potentially important and conflicting responses from other components of the carbon cycle.

Within each component's analysis, we explored both experimental and biotic explanations for observed variance. First, considering that some effects of large herbivore exclusion on carbon cycling would saturate only over long time periods (e.g. increase in carbon stored as woody vegetation) or large spatial scales (e.g. interaction of aboveground biomass and fire regime change on carbon storage and flux; Holdo et al., 2009), we anticipated that experimental plot size and duration would be important moderators of large herbivore exclusion's effects on components of carbon cycling. However, analyses of soil carbon and carbon flux did not provide support for these moderators: neither component's effect size was significantly impacted by plot size or duration (full models: soil carbon [$n = 8$], $p = 0.14$, $p = 0.28$ for duration and size, respectively; carbon flux [$n = 7$], $p = 0.31$, $p = 0.25$).

Given the robust literature on the influence of ecosystem productivity on all functions reviewed here (including carbon cycling) we also expected productivity to be an important moderator. However, individual analyses of soil carbon and carbon flux demonstrated limited and mixed support for ecosystem productivity (here, mean NDVI at each experimental location) as a significant moderator. The effect of large herbivore exclusion on soil carbon was not significantly impacted by productivity ($p = 0.13$ in full model), though that of carbon flux was ($p = 0.02$ in full model, $p = 0.03$ in reduced model; Figure 8).

The lack of explanatory power of these experimental and biological moderators may be due to lack of true effect; recent meta-analyses also found limited support for productivity in moderating effects of herbivores on plants (Jia et al., 2018; Koerner et al., 2018). However, we suspect that small sample size within components ($n = 8$ for soil carbon, $n = 7$ for carbon flux) and unreported variation in other

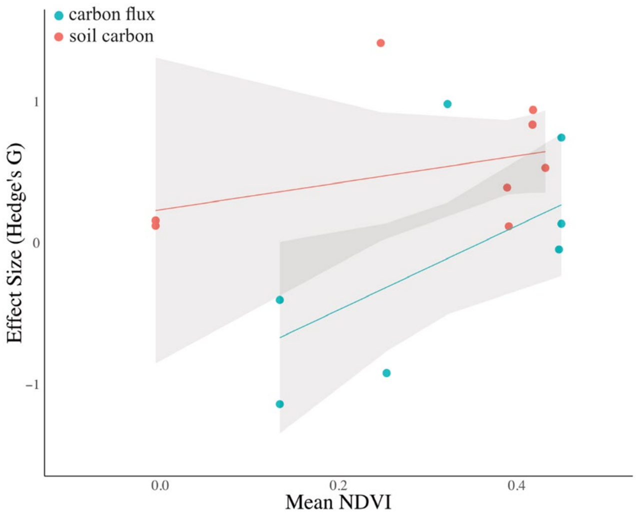

FIGURE 8 Influence of mean NDVI on effect size of large herbivore exclusion on carbon flux ($p = 0.03$, reduced model), and soil carbon ($p = 0.13$, full model). Productivity significantly moderated the effects of large herbivore exclusion on carbon flux (in blue) but not soil carbon (in red)

biotic conditions (e.g. herbivore density) limits our abilities to detect their effects on individual components of carbon cycling. Our analysis highlights a need for standardized, comprehensive data collection on all components of an ecosystem function, and detailed reporting of meta-data on exclosure systems, to understand the sources of true effect as well as variation in response to large herbivore exclusion.

4 | CONTEXT MATTERS: POSSIBLE BIOLOGICAL SOURCES OF VARIATION

It is clear from the above reviews that there is significant variability in the responses of ecosystem functions to large herbivore exclusion, likely due in part to inconsistency in large herbivores' impacts on ecosystems in general. A recent global meta-analysis of large herbivore exclosure experiments found that effects on plant performance, community composition, and community structure were variable when examined through site characteristics like productivity or climate (Jia et al., 2018). The direct effects of large herbivores on plants (via consumption) result in cascading effects on functions like carbon storage, ecosystem resilience/resistance, and plant regeneration: as the effects of large herbivores on plants are conditional on site-specific characteristics, it is thus reasonable to expect similarly variable effects on functions. Indeed, when analyzed separately, the impacts of large herbivore exclusion on aboveground biomass alone as a proxy for consumption is highly inconsistent (Appendix S3, Figure S3, Figure 1.).

It is therefore important to consider the ecological contexts of an experimental site that likely play influential roles. The presence of predators in an ecosystem may influence the effects of large herbivores and thus of their experimental removal. Large predators in east Africa mediate most large herbivores' habitat selection, likely shifting their cascading effects on functions like plant regeneration (Riginos & Grace, 2008). Predation risk alone can prompt stress-induced changes in the body compositions of herbivores, changes which can cascade to impact the composition and quality of their nutrient deposits and significantly impact nutrient cycling (Leroux, Hawlena, & Schmitz, 2012).

Herbivore density must also be considered when interpreting variability in effects reviewed here. While large wild herbivores are being impacted by global change worldwide, not all populations are declining: modern declines in hunting and predator populations, and shifts in climate and forage availability, have resulted in dramatic deer (and other game species) overabundance (Ripple et al., 2015). This can result in similarly dramatic impacts on ecosystem functions like disease transmission, ecosystem resilience/resistance, plant regeneration, carbon cycling, and nutrient cycling, among others (Côté, Rooney, Tremblay, Dussault, & Waller, 2004; Ripple et al., 2015). Herbivore identity also significantly moderates their effects on functions. By dint of their size, megaherbivores like elephants play unique roles in ecosystems and their functioning as compared to other large herbivores, while browsers and grazers also uniquely modify plant communities and the functions that precipitate from them (Fritz, Duncan, Gordan, & Illius, 2002). Indeed, as seen in our review of plant regeneration, the presence of both browsers and grazers in an ecosystem can result in opposite effects, dampening net effects on plant regeneration (Pringle et al., 2014).

Herbivore identity is likely to be particularly influential when considering the effects of domestic herbivores, as wild large herbivore loss is seldom isolated. In nature, it is often driven or rapidly followed by replacement with domestic livestock. As a result, and despite dramatic declines in wild ungulates, total large herbivore biomass on the planet today greatly exceeds historical baselines (Bar-on, Phillips, & Milo, 2018). In this review, we focused on experiments in which experimental exclosure of wild, native large herbivores occurred; however, approximately 35% of these unique experiments took place where large domestic herbivores exist and were therefore also excluded. Few formal experiments (most notably the Kenya Long-term Exclosure Experiment, KLEE) explicitly explore whether domestic herbivores fill the functional roles of large wild herbivores, by manipulating the presence/absence of both. Though domestic herbivores likely play a functionally different role than wild ones (Charles et al., 2017), major differences in effect appear to be driven more by total herbivore density than by identity (Veblen, Porensky, Riginos, & Young, 2016; Young et al., 2018).

While not included in this review, large herbivores in aquatic ecosystems also significantly impact ecosystem functions (Bakker, Pagès, Arthur, & Alcoverro, 2016). In seagrass beds, dugongs, turtles, fishes, and urchins can remove up to 90% of producer biomass (Heck & Valentine, 2006) and facilitate productivity by over 50%. Herbivorous fishes and urchins can likewise increase productivity by over 300% on coral reefs, increasing resistance to disturbances like bleaching and resilience to transition to algae-dominated reefs by maintaining lawns of small, productive algae species over macroalgae (Adam et al., 2011; Carpenter, 1986). Context like site characteristics, herbivore density, and herbivore identity also mediate the responses of functions in aquatic systems. For example, high herbivore density, like increasing populations of sea turtles in protected areas, can lead to ecosystem collapse (Christianen et al., 2014). However, despite these similarities, the effects of large aquatic herbivores on ecosystem functions are comparatively unexplored, much less joined to the existing terrestrial literature.

5 | CONCLUSIONS

The effects of large herbivores on vital ecosystem functions are increasingly used to motivate conservation of these taxa (Ripple et al., 2015). While we find strong evidence that large herbivores significantly impact many ecosystem functions, we find limited evidence for clear, predictable patterns of effect for any function (Appendix S2), even with a geographically-limited dataset (76% from temperate systems, 50% from grasslands). While this lack of predictability could be driven by inconsistent definitions for ecosystem functions in the literature, in our analysis of the carbon cycle we find similarly little predictability when a function is analyzed by its individual components, and when basic experimental and ecological properties are controlled.

In many ways, this is a surprising finding. Meta-analyses on sessile or smaller herbivore biodiversity, which are generally thought to have lower average effect on ecosystem functioning than large mobile species (Séguin, Harvey, Archambault, Nozais, & Gravel, 2014), have shown consistent negative effects of diversity loss on function. What is more, productivity covariates like climate, land-use, and nutrient availability often significantly moderate these effects (Duffy, Godwin, & Cardinale, 2017; Lefcheck et al., 2015; Soliveres et al., 2016). However, our results indicate that the functional effects of large wild herbivore removal may be less systematic than those of these smaller taxa, and indeed less predictably moderated by factors like productivity.

One likely cause of the strong variation in functional responses reported is the methodological limitation of exclosure experiments. Experimental exclosures for large taxa typically have lower control on the number and types of large taxa removed and lower replication than do similar manipulations of smaller taxa. Furthermore, as documented here, existing experiments are insufficient in size (median 400 m^2) to capture landscape-level effects like nutrient translocation, which will be better studied in large-scale natural experiments. Also problematically, the average duration of these experiments (median 6 years) means they frequently assume short-term or linear effects over time, although slow-acting responses (e.g. tree recruitment) and long-term temporal variability is known to substantially influence function (Goheen et al., 2018).

Finally, and crucially, lack of consensus on how to practically define individual functions may amplify in larger field-based experimental systems, where there are multiple metrics with which to measure the different components of a function. A function's components are all meaningful, yet are also potentially confounding when combined or misleading when considered alone. Thus, clear definitions of individual functions and the components they are comprised of is likely an essential next step. Indeed, lack of standardized terminology can be source of complexity in ecology (Fauth et al., 1996), and ecosystem function itself is interchangeably defined as service, process, and function (e.g. Franklin et al., 1981, Lamont, 1995, Srivastava & Vellend, 2005).

In addition to methodological drivers, it is likely that much of the variation observed here reflects real differences in the effects of large herbivores on ecosystem functions across ecological contexts, and which may not be captured by single covariates like ecosystem productivity. Theory suggests that effects of large herbivores on plants should vary based on a wide range of ecological contexts (e.g. productivity, climate, predator density, food chain length, presence and diversity of smaller consumers). However, these data are often difficult to collect in complex systems or considered unnecessary to a study's aims and are therefore inconsistently reported (Gerstner et al., 2017). It is consequently infeasible to interrogate all these covariates by synthesizing existing data. Relatedly, covariates on large herbivores themselves (identities and densities at a site, diet type, body size, etc.) are likely also necessary, as it is possible that the common definition of large herbivores (>5 kg) is not an ecologically meaningful grouping.

If we seek a more general understanding of the effects of large herbivores on ecosystem functions, globally or across biogeographic zones, two clear needs emerge from these reviews. First, we need more quantitative syntheses on the effects of large herbivore exclusion on individual functions. We anticipate little consensus, considering that functions contain multiple meaningful components (Figure 7a; Schmitz et al., 2014) and that data on covariates are often unavailable. However, such syntheses will at minimum explore the extent of variability by function, identify potential drivers of variation, and highlight the suite of components most useful for empirical study of each function.

A second critical need is for increased, systematic empirical exclosure research focusing explicitly on the effects of herbivore exclusion on functions. We recommend the development of a global network of exclosures across ecosystems, for which experimental plots should be at least 100 × 100 m, be replicated at least 3 times per system, and effectively exclude all herbivores >5 kg. In addition to collecting functional response data with standardized, synthesis-informed protocols, researchers would collect standardized metadata: herbivore identity and density; site productivity; presence, identity, and density of predators, small consumers, and domestic herbivores; etc. This proposed large-scale network is inspired largely by the Nutrient Network (NutNet), a collaborative experiment run by many investigators, which has leveraged standardized data collected from 5x5m exclosures across a range of environmental conditions (65 grassland sites across six continents) to detect general impacts and context-dependencies of herbivory and nutrient availability (https://nutnet.org/field_sites; Borer, Grace, Harpole, MacDougall, & Seabloom, 2017; Borer et al., 2014).

While this effort would be challenging at the plot size and spatial scale we suggest, many suitable experiments exist already. These experiments, like the KLEE, could be incorporated into the network by adopting standardized data collection protocols, informed by synthesis, for each function and relevant metadata. Once established, such a global network could detect general responses of functions to large herbivore exclusion over space and time, including large-scale and non-linear changes, and illuminate the biotic and abiotic covariates that moderate the effects of large herbivore exclusion on individual functions. Coordinated research such as this could provide experimental support for predictions of future ecosystem functioning, and support work in natural systems demonstrating the functional consequences of continued defaunation.

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AUTHORS' CONTRIBUTIONS

E.S.F. designed methods for and conducted the quantitative literature review, case study literature review and data collection, and case study analysis; she led writing of and figure generation for the manuscript. H.S.Y. contributed to literature review methods and figure generation. M.K. assisted in quantitative literature review. E.S.F., J.H.C., D.E.B., T.P.Y., M.K., and H.S.Y. each contributed one or more written sections on an ecosystem function or outstanding question. All authors provided substantive input and final approval to manuscript.

DATA AVAILABILITY STATEMENT

All data used in this review are archived on Dryad Digital Repository. This includes data used to generate descriptive statistics of all functional responses recorded within large herbivore experimental exclosures, and data used to conduct a case study analysis on the impacts of large herbivore exclosure on ecosystem carbon cycling. Both datasets can be found at https://doi.org/10.5061/dryad.3tf4mt4 (Forbes et al., 2019).

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SUPPORTING INFORMATION

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

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