

## Review

## Impacts of large herbivores on terrestrial ecosystems

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<https://doi.org/10.1016/j.cub.2023.04.024>

## SUMMARY

Large herbivores play unique ecological roles and are disproportionately imperiled by human activity. As many wild populations dwindle towards extinction, and as interest grows in restoring lost biodiversity, research on large herbivores and their ecological impacts has intensified. Yet, results are often conflicting or contingent on local conditions, and new findings have challenged conventional wisdom, making it hard to discern general principles. Here, we review what is known about the ecosystem impacts of large herbivores globally, identify key uncertainties, and suggest priorities to guide research. Many findings are generalizable across ecosystems: large herbivores consistently exert top-down control of plant demography, species composition, and biomass, thereby suppressing fires and the abundance of smaller animals. Other general patterns do not have clearly defined impacts: large herbivores respond to predation risk but the strength of trophic cascades is variable; large herbivores move vast quantities of seeds and nutrients but with poorly understood effects on vegetation and biogeochemistry. Questions of the greatest relevance for conservation and management are among the least certain, including effects on carbon storage and other ecosystem functions and the ability to predict outcomes of extinctions and reintroductions. A unifying theme is the role of body size in regulating ecological impact. Small herbivores cannot fully substitute for large ones, and large-herbivore species are not functionally redundant — losing any, especially the largest, will alter net impact, helping to explain why livestock are poor surrogates for wild species. We advocate leveraging a broad spectrum of techniques to mechanistically explain how large-herbivore traits and environmental context interactively govern the ecological impacts of these animals.

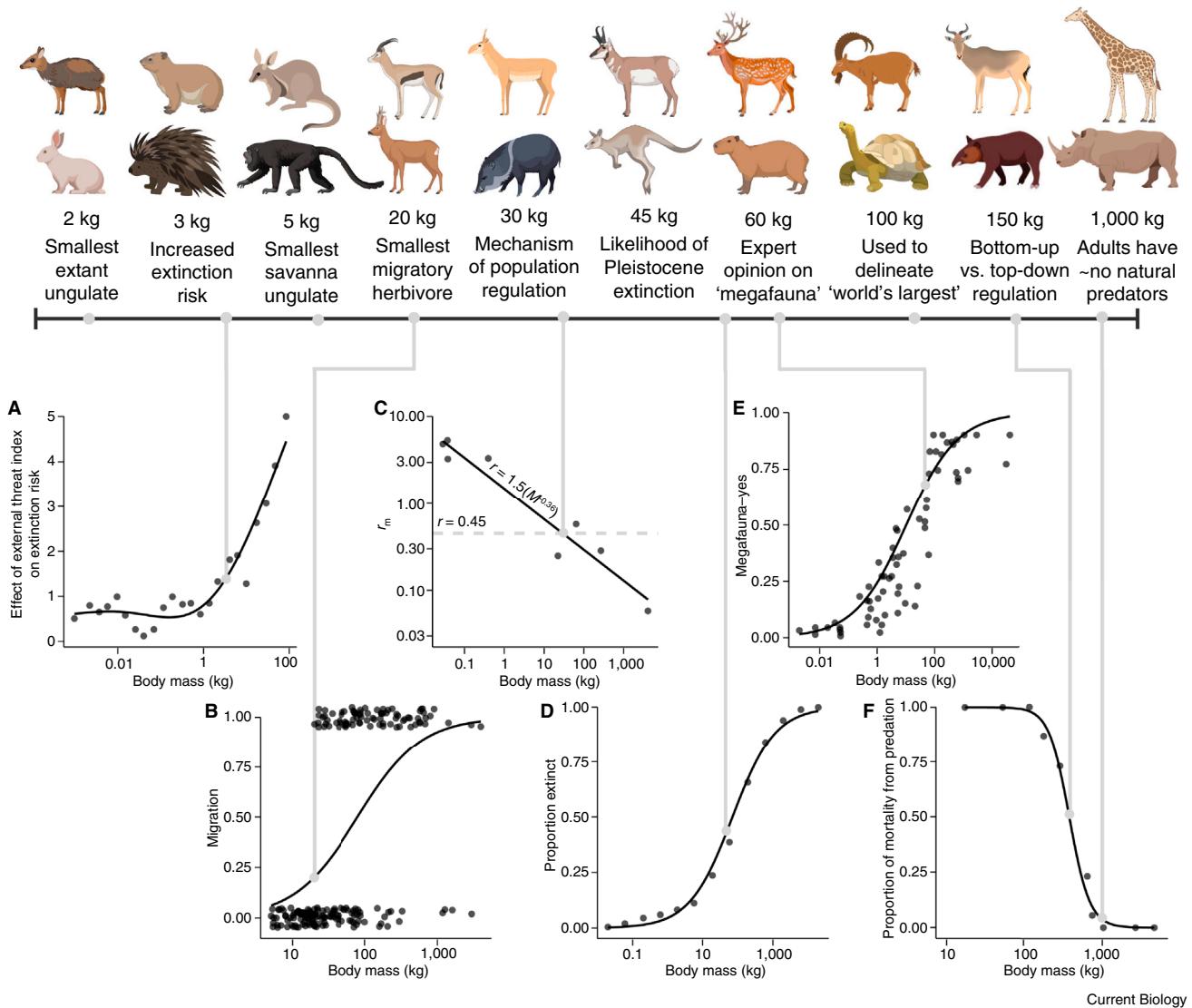
## Introduction

*“Big things such as elephants, jaguars, and tapirs tend to be neglected by ecologists, for the very reason that by being big, they lack amenability to study...I suspect that for this reason the key functions provided by the big things are underappreciated.”* - John Terborgh<sup>1</sup>

*“We live in a world analogous to an herbivore exclusion experiment, with most of the large herbivores removed.”*  
Juli Pausas and William Bond<sup>2</sup>

The quotation above from Terborgh’s 1988 essay *The big things that run the world*<sup>1</sup> captures an irony. Despite millennia of human

fascination with ‘big game,’ megafauna long occupied the margins of ecological research. Population and community ecology developed around the study of plants, invertebrates, birds, rodents, and fish; ecosystem ecology developed largely without reference to animals at all<sup>3</sup>. The comparative neglect of big animals was not for lack of reasons to study them. It was never a secret that large herbivores (plant-eating animals weighing over 2 kg)<sup>4</sup> have unique traits and can play distinctive roles in terrestrial ecosystems<sup>5–12</sup> (Figure 1). Early authors also recognized the role of large herbivores in the evolution and global expansion of hominins<sup>13,14</sup> and the role of humans in driving large herbivores extinct<sup>15</sup>. The problem was rather that large herbivores are inconvenient study subjects — difficult to manipulate and often



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**Figure 1. Size-based functional thresholds in terrestrial large herbivores.**

Top: Species representing body-size thresholds used to categorize herbivores as ‘large’. While inherently arbitrary<sup>61</sup>, many thresholds correspond to biologically meaningful distinctions (bottom, based on references cited in caption). 2 kg (chevrotain, hare): adult size of smallest extant ungulate. 3 kg (hyrax, Philippine porcupine): size above which correlates of extinction risk become more pronounced (A)<sup>56</sup>. 5 kg (rock wallaby, howler monkey): adult size of the smallest ungulates in African savanna assemblages<sup>46</sup>. 20 kg (Speke’s gazelle, roe deer): size of the smallest migratory mammalian herbivore (B)<sup>63</sup>. 30 kg (saiga, peccary): size above which intrinsic rate of increase ( $r_m$ ) drops below the level (0.45) considered necessary for intrinsic mechanisms of population regulation to evolve (C)<sup>12</sup>. 45 kg (pronghorn, red kangaroo): size above which Pleistocene extinction was much more likely (D)<sup>15</sup> and a common threshold for defining ‘megafauna’<sup>31,43</sup>. 60 kg (chital, capybara): size above which  $\geq 69\%$  of ecologists agree that an animal is ‘megafauna’ (E)<sup>61</sup>. 100 kg (ibex, spurred tortoise): threshold used to delineate the ‘world’s largest’ herbivores<sup>57</sup>. 150 kg (hartebeest, mountain tapir): size above which population regulation switches from primarily top-down (predation) to bottom-up (food limitation) in Serengeti (F)<sup>65</sup>. 1000 kg (giraffe, black rhinoceros): size above which adults are essentially invulnerable to predation (F)<sup>65</sup> and a threshold used to delineate ‘megaherbivores’<sup>18</sup>. We do not embrace any threshold in this review, instead emphasizing the diverse and frequently nonlinear ways in which body size differentiates the ecological impacts of herbivores across the spectrum shown here<sup>67,116,123</sup>. Figure created using [BioRender.com](#).

even to observe, intractable for testing theory, “not the stuff of NSF grants”<sup>1</sup>. Moreover, the diminished abundance of large herbivores across much of the world by the mid-20<sup>th</sup> century<sup>2</sup> diluted and dispersed their ecological impacts, making them easier to ignore.

By 1988, that oversight was already starting to fade. A series of syntheses over the following decade placed large-herbivore ecology in a broad conceptual framework and identified common patterns across ecosystems and continents<sup>16–23</sup>. Attention

to the ecological importance of body size<sup>18,24,25</sup> and accumulating evidence that large herbivores could be keystone species<sup>26–28</sup> reinforced the value of studying wild large herbivores, and an ever-expanding methodological toolkit has made it ever easier to do so. Most recently, interest in ‘rewilding’ to recover the lost functional roles of extinct large herbivores<sup>29–34</sup> has fueled attempts to pinpoint what those roles actually are, and to what extent modern herbivore assemblages approximate ancient ones<sup>35–39</sup>. The mainstreaming of megafauna in ecology

has produced many exciting discoveries and spawned a wealth of reviews, meta-analyses, and models<sup>40–55</sup>. Still, many questions remain unanswered. Recent reviews imply a consensus that wild large herbivores are pivotal in regulating ecosystem functioning but do not always clearly distinguish isolated case studies from repeatable general rules.

The rapid growth of this literature has been motivated in part by the goal of understanding, predicting, and mitigating anthropogenic global change. Large herbivores are disproportionately prone to extinction from human activity<sup>56,57</sup>. Quaternary extinctions have been so size-selective that large herbivores are smaller now than at any time in the last 30 million years<sup>58</sup>. 60% of the 75 mammalian large-herbivore species weighing  $\geq 100$  kg are threatened with extinction<sup>57</sup>, as are all 12 species of mega-herbivore ( $\geq 1000$  kg) and 83% of all tortoise species<sup>59</sup>. A fifth of these species are listed as critically endangered, with numbers ranging from a few tens to a few thousands globally, and may thus be functionally extinct. Meanwhile, domesticated large herbivores continue to increase in density and distribution, often displacing wild counterparts from their remaining strongholds<sup>57</sup>. How will the decline and replacement of wild large herbivores affect ecosystems? What constraints limit ecologists' ability to answer that question? And what are the implications for conservation, restoration, and management?

This review has three main aims. First, we identify a set of general rules that have solidified over the last decade — inferences about the ecosystem impacts of large herbivores that have repeatedly and rigorously been tested in nature and that apply with few exceptions worldwide (Table 1). Second, we survey important but intractable problems and emerging research frontiers. Third, we highlight the need for process-based and species-specific knowledge to break down longstanding barriers to generalization, prediction, and applied relevance. We argue that mechanistic understanding of large-herbivore impacts is generally weak, even in most experimental studies, and that this contributes to a disconnect between the current state of the field and its aspirations. We are cautiously optimistic that this gap can be closed, and we conclude by outlining some promising strategies.

## Generalizations about the roles and impacts of large herbivores

### **Body size governs impact, and small herbivores do not compensate for large herbivores**

A premise of focusing on impacts of large herbivores is that big-bodied herbivores are a category apart from smaller vertebrate and invertebrate herbivores. This premise holds despite the lack of any universal criterion for defining where 'small' ends and 'large' begins<sup>60,61</sup>. Dramatic changes in functionally relevant traits occur at different body sizes (Figure 1). For example, species  $>3$  kg are markedly more at risk of extinction<sup>56</sup>; species  $>7$  kg are disproportionately targeted by human hunters<sup>62</sup>; migratory behavior is confined to species  $>20$  kg<sup>63</sup>, which also have much larger home ranges<sup>64</sup>; species  $>30$  kg are unlikely to evolve intrinsic behavioral or physiological mechanisms of population regulation<sup>12</sup>; populations of species  $>150$  kg are far more likely to be limited by food than by predators<sup>65</sup>; and species  $>1000$  kg are essentially invulnerable to nonhuman predators<sup>65</sup>. Large herbivores are often simply defined taxonomically, which

is also justifiable. Ungulates (Artiodactyla, Perissodactyla) account for 50% of wild terrestrial mammal biomass, elephants (Proboscidea) add 8%, and kangaroos and other marsupial herbivores (Diprotodontia) add another 7%<sup>66</sup>. In sum, the variety of size-based functional thresholds and the global dominance of four taxonomic orders of indisputably big mammalian herbivores suggest that 'large herbivore' is an ecologically meaningful heuristic category — but that it is even more useful to consider body size as a continuous variable.

Indeed, an overarching generalization that we revisit in various specific contexts throughout this review is that body size regulates the form, strength, and direction of herbivore impacts in ways that quantitatively and qualitatively distinguish large herbivores from smaller herbivores (and from each other). These differences arise from the allometric scaling of food requirements<sup>41</sup>, behavior<sup>64,67</sup>, and morphophysiological constraints<sup>68,69</sup>, along with assorted traits and capabilities that are unique to very large herbivores<sup>70–77</sup>. Such size-based differentiation in 'requirement' and 'impact' niches<sup>78</sup> is key for understanding the origin and functional importance of large-herbivore diversity. Sympatric large-herbivore species differ in size (which almost certainly reflects competitive constraints on coexistence), and large species account for the greatest share of biomass and energetic demand in intact communities (Figure 2). This in turn suggests that bigger herbivores should exert stronger per capita and net impacts, and that smaller herbivores should not be able to fully compensate for the loss of larger ones<sup>79</sup>.

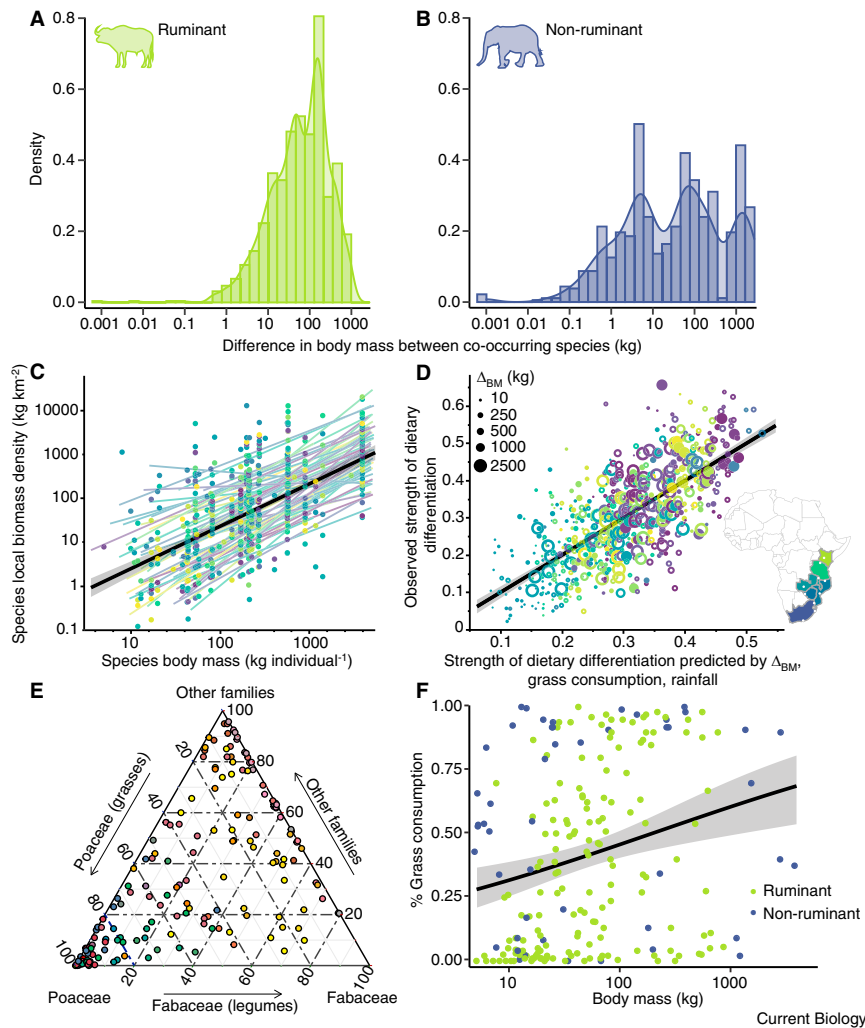
Support for these propositions comes from enclosure experiments that remove large herbivores but are permeable to small species — the primary method for causal inference about large-herbivore impacts (Figures 3–5). Hundreds of enclosure studies worldwide have revealed countless direct and indirect effects of large herbivores<sup>80–93</sup>, and we know of no long-term study that has failed to detect any effect. These results, and similar ones from defaunated landscapes, such as forests where hunters have eliminated peccaries and monkeys but spared the rodents<sup>94–96</sup>, show that small consumers undercompensate for the loss of large herbivores. Densities of small mammals and insects increase in enclosures and overhunted forests, but not to the point of matching the biomass and energetic demand of large herbivores<sup>97–100</sup>, and there are only a few reported cases of full compensation for even one response variable<sup>101</sup>. Similarly, small ungulates are more abundant in size-selective enclosures<sup>102</sup> and megaherbivore-free landscapes<sup>79</sup> but do not reproduce the impacts of larger species<sup>103–108</sup> (Figure 5).

### **Different large herbivores have different diets, implying functional complementarity**

Plant biomass varies in accessibility, digestibility, nutrient content, and toxicity. Large herbivorous mammals vary along a continuum from grazers that eat monocots (mainly grasses) to browsers that do not; 'mixed feeders' eat substantial amounts of both<sup>109–111</sup> (Figure 2E). This grazer–browser spectrum is rooted in traits of both herbivores (e.g., dentition, anatomy<sup>112</sup>) and plants (e.g., grasses with high tensile strength and abrasive phytoliths that non-grasses lack<sup>113,114</sup>). The modality of this spectrum varies, and species' positions along it can differ in time and space, but the general pattern is universal both across large-herbivore lineages and within local assemblages, suggesting its importance in maintaining large-herbivore diversity<sup>111,115</sup>.

**Table 1. Generalizations about the impacts of large herbivores in terrestrial ecosystems.**

Generality	Mechanisms	Manifestations	Citations
Body size regulates herbivore requirements and impacts	<ul style="list-style-type: none"> <li>– Allometric scaling of energetic requirements, life history, behaviors, predation vulnerability.</li> <li>– Bigger herbivores reach higher biomass, eat more phytomass.</li> <li>– Traits unique to extremely large herbivores.</li> </ul>	<ul style="list-style-type: none"> <li>– Functional thresholds occur at different body sizes (Figure 1).</li> <li>– Small herbivores under-compensate for large ones (Figure 5).</li> <li>– Elephants are uniquely able to kill adult trees but less selective for shoots, seedlings.</li> </ul>	18,64,67–69,73,77,100
Dietary differentiation	<ul style="list-style-type: none"> <li>– Herbivore and plant traits constrain plant taxa and tissues eaten.</li> <li>– Competition prevents coexistence of species with identical diets and promotes adaptive differentiation of traits that constrain diet.</li> </ul>	<ul style="list-style-type: none"> <li>– Grazer–browser spectrum (Figure 2E,F).</li> <li>– Herbivore species eat different plant species (Figure 2D,E).</li> <li>– Species differ in selectivity for nutrient-rich tissues.</li> <li>– Differences scale with body size (Figure 2); big species need more food, cannot be as selective.</li> <li>– Species are not functionally equivalent.</li> </ul>	18,54,69,114,123,124,128,129,135
Top-down control of plants	<ul style="list-style-type: none"> <li>– Lethal, nonlethal consumption.</li> <li>– Mutualist suppression.</li> <li>– Offsetting benefits (dispersal, enemy suppression, nutrient inputs).</li> </ul>	<ul style="list-style-type: none"> <li>– Lower plant performance, biomass, density.</li> <li>– Reduced tree cover.</li> <li>– Depression of aboveground net primary production (with localized exceptions).</li> </ul>	10,19,47,54,85,96,105,139,147,158,162
Alteration of plant species composition	<ul style="list-style-type: none"> <li>– Differences in palatability, resistance, tolerance leads to ‘increaser’ or ‘decreaser’ species.</li> <li>– Modified plant–plant interactions.</li> </ul>	<ul style="list-style-type: none"> <li>– Large herbivores filter plant communities, leading to species replacement but limited net change in richness.</li> <li>– Positive effects on richness occur mainly in productive grasslands.</li> </ul>	47,48,172,184,185,190,194–196
Modulation of fire and its impacts	<ul style="list-style-type: none"> <li>– Reduced fuel load, continuity, composition.</li> <li>– Altered plant architecture.</li> <li>– Feedbacks from effects on food quantity, quality.</li> </ul>	<ul style="list-style-type: none"> <li>– Large herbivores reduce fire frequency, intensity, and/or extent.</li> <li>– Functionally diverse herbivore guilds best suppress fuel loads.</li> <li>– Fire and browsers synergistically suppress trees.</li> </ul>	154,182,199,203–205,207,213
Transport and nutrient cycling	<ul style="list-style-type: none"> <li>– Dung, urine, and death lead to long-distance transport of matter.</li> <li>– Diet affects content of inputs.</li> <li>– Traits that lower palatability also slow decomposition.</li> </ul>	<ul style="list-style-type: none"> <li>– Herbivore-vectored transport differs from abiotic drivers.</li> <li>– Content, distance, and spatiotemporal pattern of inputs scale with body size.</li> <li>– Simple rules about effects on nutrient recycling rates are not general.</li> </ul>	219,226,227,229,230,233,357,362
Indirect suppression of small animals	<ul style="list-style-type: none"> <li>– Plant depletion limits food and structure available for other consumers.</li> <li>– Effect size scales with regrowth rate.</li> </ul>	<ul style="list-style-type: none"> <li>– Suppression of small herbivores propagates through food webs.</li> <li>– Stronger effects at low primary production.</li> <li>– Exceptions: specialized herbivore symbionts, some habitat-modification effects.</li> </ul>	97,236–238,242,247,248
Risk alters behavior, cascades are variable	<ul style="list-style-type: none"> <li>– Large herbivores perceive correlates of predation risk.</li> <li>– Response hinges on herbivore vulnerability (size), predictability of risk, strength of tradeoffs.</li> </ul>	<ul style="list-style-type: none"> <li>– Sustained avoidance of risky areas releases plants.</li> <li>– Unpredictable risk, invulnerable herbivores, strong fitness tradeoffs, and avoidance in time dampen trophic cascades.</li> </ul>	77,254–257,259–261,263–266,268,269
Increased ecosystem heterogeneity	<ul style="list-style-type: none"> <li>– Herbivore activity is non-uniform in space and time.</li> <li>– Feedbacks amplify heterogeneity arising from variation in density, activity.</li> </ul>	<ul style="list-style-type: none"> <li>– Geology, water proximity, etc. alter herbivore densities and their impacts.</li> <li>– Game trails, foraging hotspots, etc. ingrain impacts atop underlying gradients through repeated use.</li> </ul>	73,272,275,276,278,279,281,282
Livestock are poor proxies for wild large herbivores	<ul style="list-style-type: none"> <li>– Domestic species differ from even close wild relatives in traits.</li> <li>– Livestock attain high density.</li> <li>– Livestock assemblages have less trait diversity than wild ones.</li> </ul>	<ul style="list-style-type: none"> <li>– Trait differences and protection of animals from enemies and resource limitation results in different foraging, densities, impacts.</li> <li>– Many wild large herbivores have no domestic analogue.</li> <li>– Management can relax these differences.</li> </ul>	90,142,176,284,293–295,297,298,302



**Figure 2. Body size structures large-herbivore assemblages and diets.**

(A,B) Co-occurring large herbivores differ in body size. Histograms show distribution of body-mass differences between pairs of ruminant (A) and nonruminant (B) large herbivores (species  $\geq 2$  kg that eat  $\geq 80\%$  plants<sup>445</sup>) that co-occur in any location in Africa<sup>446</sup>. Species of very similar size rarely co-occur (modal differences of  $\sim 100$  kg in ruminants and  $\sim 10$ ,  $\sim 100$ , and  $\sim 1000$  kg in non-ruminants), suggesting that size differentiation fosters coexistence. (C) Intact large-herbivore assemblages are dominated by large-bodied species. Estimates of species' biomass density from 60 protected areas in 17 African countries<sup>447</sup> are plotted as a function of species' body mass (BM)<sup>448</sup>. Colors indicate locations; thin lines show trend within locations, black line shows overall trend ( $r^2 = 0.33$ ). Scaling densities by metabolic rate ( $4.21 \times \text{BM}^{0.77}$ ) to reflect energetic requirements does not change the pattern ( $r^2 = 0.22$ ). (D) Co-occurring large-herbivore species differ in diet composition (relative abundance of plant taxa, from DNA metabarcoding<sup>123</sup>), and difference in body size ( $\Delta_{\text{BM}}$ ) predicts the strength of this differentiation. Each point corresponds to a pair of sympatric herbivore species from a given location in Africa (sized by  $\Delta_{\text{BM}}$ , colored by season and location as per inset map); solid points are pairs with similar digestion (ruminant or nonruminant), open points are ruminant–nonruminant pairs. X-axis shows relative strength of differentiation predicted by a regression model with  $\Delta_{\text{BM}}$ , % grass consumption, and rainfall as fixed effects and random intercepts for location<sup>123</sup>; y-axis shows observed strength of differentiation ( $r^2 = 0.52$ ).  $\Delta_{\text{BM}}$  alone explains 5% of variance ( $p < 0.0001$ ). (E) Ternary plot extending the grazer–browser spectrum of dietary variation. Points show diets of different populations of 30 African herbivore species<sup>123</sup> (colors indicate species). Left axis shows consumption of grasses (Poaceae), with some species eating almost 100% grasses (grazers) and others eating almost none (browsers). Nongrass forage is divided among legumes (Fabaceae, bottom) and all other plant families (right), showing how taxonomic resolution reveals additional dimensions of dietary variation. (F) Body size affects species' position on the grazer–browser spectrum, with grass consumption being significantly higher on average in larger-bodied species. Points are 164 large-herbivore species in a global synthesis<sup>128</sup>.

(right), showing how taxonomic resolution reveals additional dimensions of dietary variation. (F) Body size affects species' position on the grazer–browser spectrum, with grass consumption being significantly higher on average in larger-bodied species. Points are 164 large-herbivore species in a global synthesis<sup>128</sup>.

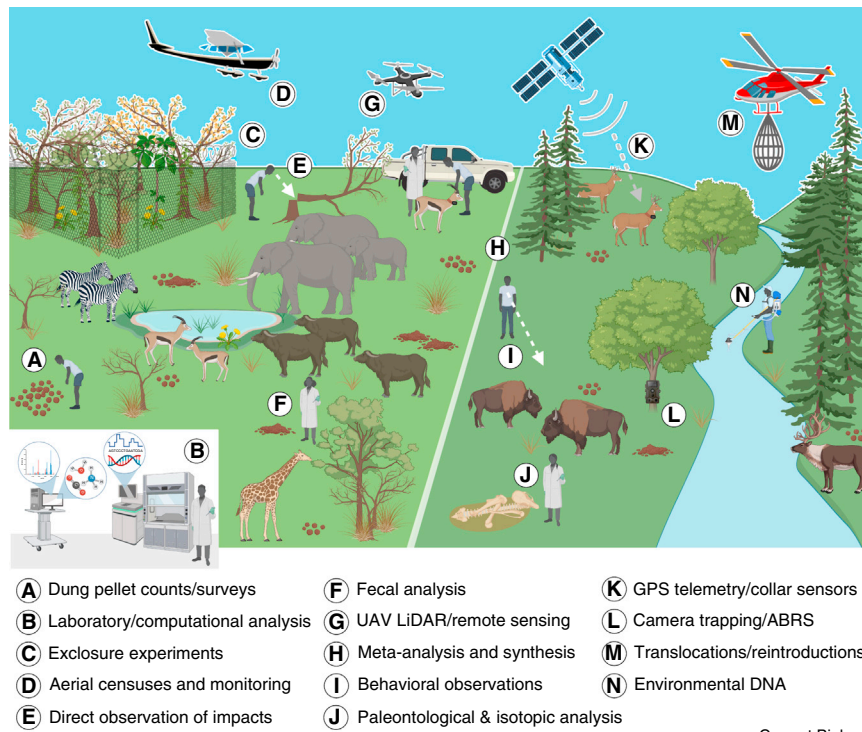
Sympatric large herbivores also consistently differ in the taxonomic composition of their diets<sup>116–123</sup> (Figure 2E). This form of dietary differentiation also arises from the interplay of plant and herbivore traits<sup>114</sup> and is nested within the grazer–browser spectrum. The latter is the dominant axis of resource partitioning, reflecting the ancient split between monocots and other plant lineages; along that axis, different large herbivores eat different mixes of species. Further nested within taxonomy, large herbivores differentially select plant tissues based on phenology, nutritional quality, and height<sup>124–126</sup>. These multiple axes of separation minimize dietary redundancy among co-occurring large herbivores, despite species' broad fundamental niches, shared use of plant species, and often parallel food preferences<sup>123,127</sup> (Figure 5C).

Body size mediates separation along all of these axes, being positively correlated with grass consumption (Figure 2F), foraging height, and degree of differentiation in dietary species composition (Figure 2D) and negatively correlated with average diet quality<sup>18,67,69,112,114,123,128</sup>. Negative scaling of diet quality

with body size (the Jarman-Bell effect<sup>124,129</sup>) arises from herbivores' selection of both plant taxa and plant tissues and is a strong generality, although its classic physiological explanations<sup>130</sup> — long considered axiomatic — have recently been challenged<sup>69,131–133</sup>. Contrary to theory<sup>134</sup>, however, recent work has found no link between body size and dietary taxonomic or phylogenetic diversity; niche breadth on these axes appears to be remarkably constrained<sup>119,122,123,135,136</sup>.

Lack of dietary redundancy implies a lack of functional redundancy, suggesting that species loss or addition should alter the net impact of the entire assemblage, that diverse assemblages should directly affect more plant species, and that the range of impacts on vegetation should increase with the size range of the herbivore assemblage. The available data support these hypotheses. Grazers and browsers have predictably different impacts on herbaceous and woody plants<sup>54</sup>. Big herbivores eat more stem, bark, and other fibrous material<sup>18,114</sup>, which removes support for photosynthetic tissue and produces strong effects on vegetation structure<sup>72,73</sup>.





**Figure 3. How ecologists study the impacts of large herbivores.**

Advances in understanding large-herbivore impacts have been catalyzed by a mixture of time-tested field methods and new technical tools. Exclosures (C) remove herbivores above a certain size from experimental plots, enabling cause-effect inference about how herbivores affect their environments. Exclosure results are clarified and deepened by field observations (E) and data on factors such as herbivore density (A,D), diet (F,I,J), and behavior (I,K,L). Camera traps (L) are used both for monitoring and as automated behavioral response systems (ABRS) for experiments involving playbacks of audio cues. Unoccupied aerial vehicles (UAVs) carrying light-detection and ranging (LiDAR) and other sensors (G) can compensate for the limited size of exclosures by enabling comparative analysis at much larger scales. Syntheses of field data (H) enable researchers to test the generality of local findings across biomes and continents (stripe distinguishes an African landscape, left, from a high-latitude one, right). Translocations (M) create unique opportunities for quasi-experimental investigation of how introducing individuals or populations affects ecological dynamics. DNA and other compounds sampled from the environment (N), feces (F), and bodies (J) can be analyzed in laboratories (B), offering unprecedented insights into large-herbivore ecology. Figure created using [BioRender.com](https://www.biorender.com).

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### Large herbivores reduce the vital rates, density, cover, and biomass of plants

Classic theory suggested that herbivores might have weak effects on plants in three-level food chains, such as those involving large herbivores and carnivores<sup>137,138</sup>. Not so. A global meta-analysis of exclosure studies found negative effects of wild herbivores on plant survival, reproduction, abundance, and biomass<sup>47</sup>. Syntheses of exclosure data from temperate forests and tropical savannas likewise show strong negative effects of large herbivores on plant cover, density, growth, survival, and reproduction<sup>46,54,139–141</sup>. Within and across these experiments, large-herbivore biomass predicts the strength of the plant responses<sup>54,139,140,142</sup>. At larger scales, mass die-offs of large herbivores increase ecosystem tree cover<sup>143,144</sup>, and woody encroachment in Africa is weaker in areas with abundant large herbivores<sup>145</sup>, mirroring results from exclosures. Although grazers are expected to benefit trees in savannas by releasing them from competition with grass, negative net effects of large herbivores on trees are common even in grazer-dominated systems and despite suppression of grass biomass<sup>104,105,139,145–148</sup>. This suggests that indirect facilitation of trees by grazers is generally weak and outweighed by even modest browsing; it probably also reflects the fact that there are few pure grazers (Figure 2E,F) and that food-limited grazers at high densities both eat and trample young trees<sup>123,149–152</sup>.

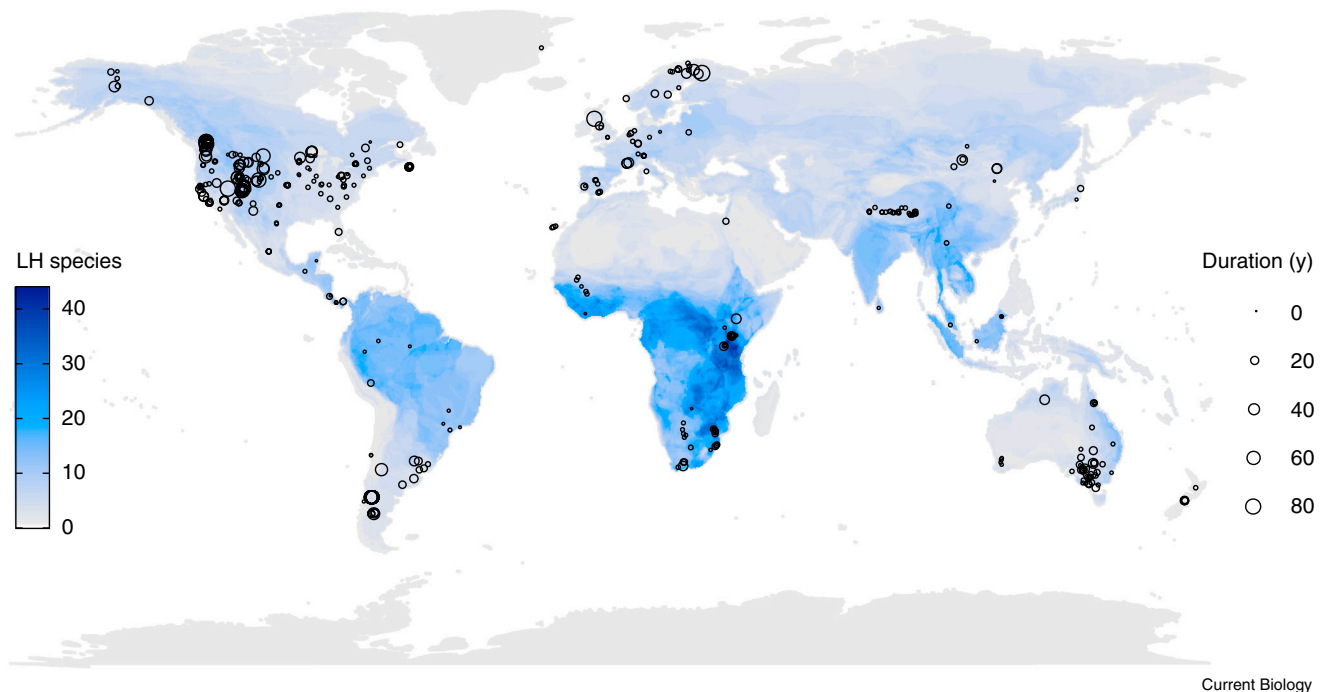
These net effects of entire large-herbivore assemblages are products of component interactions that differ in strength and direction among herbivore species. For example, regulation of savanna tree cover by browsers arises from leaf consumption and reduced capacity for growth and reproduction, from flower consumption and indirect suppression of pollinators, and

from recruitment bottlenecks and mortality at different life stages<sup>85,92,103,104,147,153–155</sup>. These negative effects are only partially offset by benefits of seed dispersal, grass removal by grazers, and indirect suppression of smaller leaf- and seed-eating consumers<sup>85,103,154,156</sup>.

Large-scale effects of large herbivores on aboveground net primary production are generally negative, but can be neutral or positive under limited conditions, notably in grasslands with moderate intensities and long histories of grazing<sup>17,142,157–160</sup>. By contrast, localized large-herbivore-induced increases in primary production are common. Grazing lawns of palatable, defoliation-tolerant short-grass species emerge in response to intense grazing worldwide. These hotspots of forage and high visibility attract large herbivores, which deposit urine and feces, further enhancing primary productivity in a positive-feedback loop that can be sustained indefinitely<sup>10,27,72,75,161–168</sup>. Although less studied, chronic browsing can induce effects similar to grazing lawns in woody plants and forbs<sup>169–171</sup>.

### Large herbivores alter plant communities but have weak effects on species richness

Large herbivores suppress some plant species (“decreasers”) to the benefit of others (“increasers”), and effects of large herbivores on plant community composition are essentially universal<sup>17,46,93,140,172–179</sup>. A plant’s response to large herbivores reflects the interplay of its palatability (i.e., herbivore preference) and its robustness to herbivory as conferred by avoidance (escaping consumption), resistance (reducing consumption), and tolerance (withstanding consumption) mechanisms<sup>180–182</sup>. Palatable plants with low robustness tend to be decreasers; unpalatable or robust plants tend to be increasers. Palatable plants that are tolerant (as in grazing lawns) enable positive feedbacks



**Figure 4. Distribution of research on large-herbivore impacts in relation to their diversity.**

Locations of 492 studies experimentally excluding vertebrate herbivores<sup>47–49</sup>, superimposed on a map of large-herbivore (LH) species richness ( $\geq 2$  kg,  $\geq 80\%$  plant-based diets) based on range maps from the IUCN<sup>449</sup>. Circle size denotes experimental duration. Research is concentrated in low-diversity temperate ecosystems, with gaps in tropical America, western and central Africa, and eastern and southern Asia. Multidecadal studies are scarce, particularly in the tropics.

between large herbivores and primary productivity<sup>22</sup>. Palatability and robustness both arise from many traits and physiological processes, notably photosynthetic capacity, growth rate and form, leaf nitrogen, fiber, spines, and phenolic compounds. Selective foraging in relation to these attributes filters plant species composition at local to biogeographic scales<sup>182–186</sup> and alters trait manifestation at within-individual to macroevolutionary scales via phenotypic plasticity and natural selection<sup>186–189</sup>.

Large herbivores also modify plant–plant interactions, resulting in indirect (non-consumptive) effects. Many traits that make plants unpalatable or robust to large herbivores are competitively disadvantageous (e.g., short stature, high defensive investment). Accordingly, plants that are rarely eaten may nonetheless respond strongly to large herbivores due to the suppression of their competitors. Some facilitative interactions that occur in the presence of large herbivores (e.g., associational resistance) become neutral or competitive in their absence<sup>190–192</sup>, while other facilitative interactions become stronger when large herbivores are scarce (e.g., release of shrubs provides structural support for vines)<sup>106</sup>.

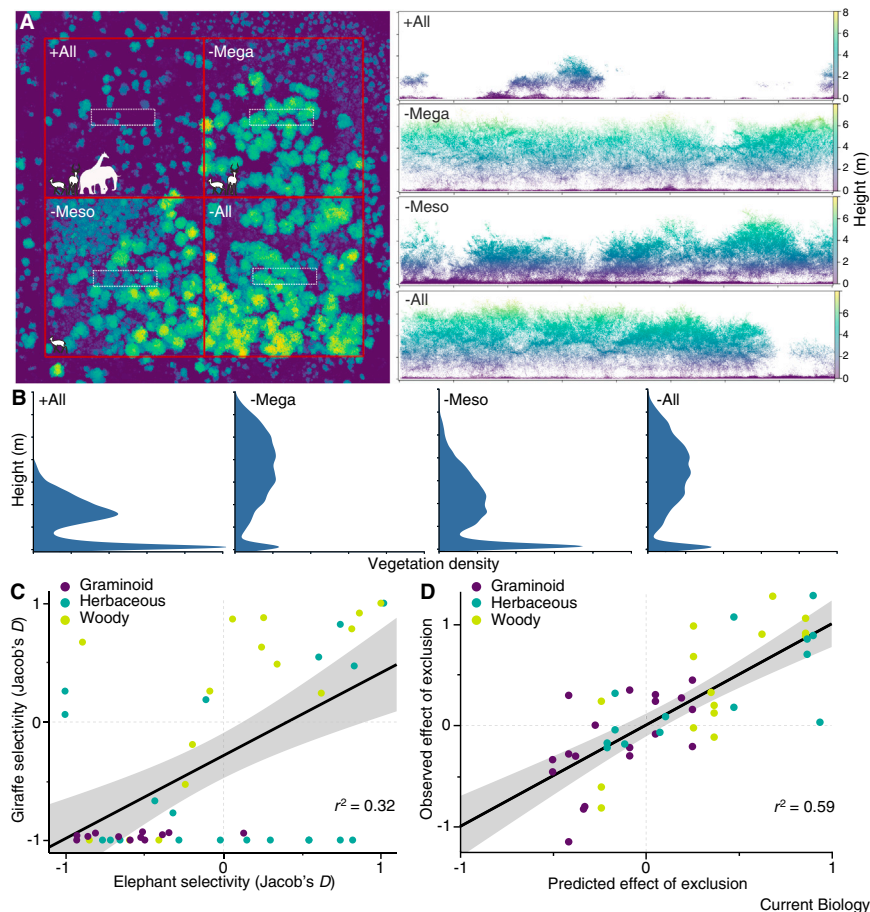
This trait-based variability in the sign of direct and indirect impacts helps to explain the weak net effect of large herbivores on plant richness: large herbivores tend to shift the identity and abundance, rather than the number, of plant species. The most comprehensive global meta-analysis to date<sup>47</sup> found no effects of herbivory on richness across biomes. Diversity-enhancing effects occur mainly in grasslands and only under certain conditions. This contingency is unusually well understood and depends on primary productivity and grazing history. In places

with low productivity and short grazing histories, large herbivores have little effect on diversity; under the opposite conditions, large herbivores increase diversity by suppressing tall, competitively dominant plant species and releasing subordinates from competition for light<sup>16,48,107,193–196</sup>.

#### **Large herbivores moderate fire regimes, and herbivore–fire feedbacks regulate vegetation dynamics**

Large herbivores and fire are both generalist consumers of plant biomass that differ in ‘food preference’ but nonetheless compete<sup>182,197</sup>. With limited exceptions<sup>198</sup>, large herbivores reduce fire frequency, intensity, or extent by reducing quantity, flammability, composition, or continuity of fuel<sup>198–201</sup>. A global review found that while large herbivores sometimes had no effect on fire, they very rarely had positive effects (and those were by livestock)<sup>201</sup>. In Africa, fire decreases with large-herbivore biomass at local to continental scales, especially in drier landscapes<sup>145,202</sup>. Herbivore species and assemblages that eat both trees and grasses control fuel most effectively<sup>54,201</sup>. These modern data are consistent with evidence that fire increased globally after the Pleistocene megafaunal extinctions<sup>203–205</sup>.

Large herbivores alter the impacts of fires on plants and vice versa<sup>206</sup>. While fire depletes absolute forage quantity, nutritious postfire regrowth attracts grazers and browsers alike<sup>207–211</sup>, intensifying local herbivore–fire interactions and feedbacks<sup>148</sup>. Browsing elevates trees’ vulnerability to fire by stunting growth<sup>212</sup>. Elephants in particular interact synergistically (super-additively) with fire to increase tree mortality<sup>213–216</sup>. By contrast, heavy grazing creates stubble and bare soil, which limits fire and alleviates tree–grass competition<sup>217</sup>. As a result,



**Figure 5. Probing exclosures with complementary data streams for mechanistic insight.**

The UHURU experiment in Kenya<sup>450,451</sup> uses size-selective fencing to exclude nested subsets of large herbivores: +all plots are unfenced, -mega excludes only species  $\geq 1000$  kg (elephant and giraffe), -meso excludes all species  $\geq 10$  kg, and -all excludes all species  $> 2$  kg. (A,B) LiDAR imagery (A) shows effect of each treatment on vegetation structure and density (B) after 12 years (lateral views and density distributions correspond to white rectangles in overview). Divergent effects of each treatment show that small large herbivores do not fully compensate for bigger ones. (C) Elephant and giraffe, the megaherbivores, eat significantly different diets at this site but share preference for many plant taxa. Points are 50 plant taxa (colored by growth form) in the diet of at least one species; herbivore selectivity (Jacob's  $D$ ; positive values indicate selection, negative values avoidance) was calculated by combining diet data<sup>135,285</sup> with data on the relative availability of each plant<sup>451</sup>. (D) A multiple-regression model with 6 predictors (elephant selectivity, plant spinescence, and plant energy, Mg, Na, and Zn contents) explained 59% of variation in plant response to megaherbivore exclusion, suggesting that herbivore impacts can be predicted by a combination of herbivore preference and plant traits. Response to megaherbivore exclusion was calculated for each plant population (points) as  $\ln(N_{-mega}/N_{+all})$ , where  $< 0$  indicates lower abundance in exclosures and vice versa; x-axis shows responses predicted by the model, y-axis shows observed responses. Elephant selectivity alone was a stronger predictor of plant response ( $r^2 = 0.36$ ,  $p < 0.0001$ ) than was giraffe selectivity alone ( $r^2 = 0.17$ ,  $p = 0.003$ ).

savanna tree cover can sometimes covary positively with grazer abundance, despite the generally negative net effects of large herbivores on trees as a whole<sup>218</sup>.

### Large herbivores redistribute large quantities of organic matter, altering nutrient cycling

Transport of carbon, nutrients, and seeds by large herbivores<sup>42,52,53,219–222</sup> differs from abiotic mechanisms such as gravity, wind, and flooding in quantity, spatiotemporal pattern, and composition<sup>223,224</sup>. To list just a few salient examples, hippos defecate  $> 3,000$  tons of organic matter into Kenya's Mara River each year<sup>76</sup>, and white rhino redistribute  $> 25$  kg N  $\text{ha}^{-1}$  year<sup>-1</sup> into dung middens<sup>225</sup>. Large herbivores move assimilated nutrients in their bodies that die and decompose<sup>226</sup>. Giant tortoises and elephants deposit hundreds of seeds per dung pile over distances up to 4 and 67 km, respectively<sup>227,228</sup>.

Body size distinguishes large herbivores from other animal vectors and large-herbivore species from one another. The allometric scaling of space use<sup>64,67</sup> and diet quality (and hence fecal composition<sup>229</sup>) suggests that smaller large herbivores should distribute more concentrated nutrients more evenly over smaller areas. Multiple studies support this idea<sup>77,230,231</sup>. The biggest large herbivores have few natural predators (Figure 1) and thus carry nutrients across areas of high predation risk<sup>77</sup>. Body size also has implications for relative nutrient supply<sup>232</sup>. Larger herbivores require greater amounts of phosphorus to support bone

mass, which affects fecal and carcass stoichiometry and the ratio of nitrogen vs. phosphorus inputs<sup>226,230,233,234</sup>.

Selective foraging and subsequent excretion, defecation, and death alter nutrient cycling, but effect size and direction vary. Several general principles influence these effects: large herbivores select nutritious foliage, dung and urine nutrient content scales with diet composition, and plant traits that reduce palatability also slow decomposition<sup>22,45,188,235</sup>. Yet, simple rules extrapolated from these premises — that grazers accelerate and browsers decelerate cycling, and that large herbivores hasten cycling in fertile systems but slow it in infertile ones — appear less general than once thought in light of current data<sup>233</sup>. A recent framework of context-dependent mechanisms by which large herbivores modulate nutrient recycling rates has proposed more nuanced generalizations that require further testing<sup>233</sup>.

### Large herbivores indirectly suppress smaller animals

Large herbivores generally reduce density and diversity of smaller animals<sup>99,236–239</sup>, including other large herbivores<sup>102,240</sup>. These effects can be direct (e.g., ingestion of insects on foliage<sup>98,237,241</sup>) but most are indirect and essentially competitive. Plant biomass eaten or modified by large herbivores becomes unavailable to other primary consumers, which then propagates up food chains. For example, large herbivores suppress pollinators by reducing flower abundance and diversity<sup>92</sup> and rodents by reducing plant density and seed set<sup>97,242,243</sup>, which in turn



limits predators of these species<sup>84,244</sup>. Exceptions to this rule include obligate associates of large herbivores (e.g., parasites, dung beetles<sup>245–247</sup>) along with various idiosyncratic and often localized facilitative interactions (e.g., species benefitting from ecosystem engineering by megaherbivores)<sup>248,249</sup>. The strength of negative indirect effects scales negatively with aboveground net primary production, dampened by the greater regenerative ability of plants in more productive systems<sup>84,238</sup>.

### **Large herbivores respond to predation risk, which often alters their impacts**

Predation risk alters large-herbivore behavior, which can impact plants and ecosystem functions (behaviorally mediated trophic cascades)<sup>250</sup>, but the strength of these cascades varies and is sometimes negligible<sup>251–255</sup>. That large herbivores are responsive to real and perceived predation risk, even after decades of predator absence<sup>256</sup>, is indisputable. A more useful emerging generalization is that the strength and form of herbivore response — and hence trophic cascades — depends on the spatiotemporal predictability of risk and the ability of large herbivores to adjust their behavior in ways that mitigate vulnerability without diminishing impact<sup>165,254,257–263</sup>. Experimental or quasi-experimental evidence of trophic cascades involving large herbivores and carnivores exists from multiple continents<sup>77,264–266</sup>, as do studies finding no evidence of trophic cascades despite strong predator-induced changes in herbivore behavior or density<sup>261,267–269</sup>. As ever, body size matters: very large herbivores are less vulnerable to non-human predators (Figure 1F) and thus less behaviorally sensitive to risk<sup>77,165</sup>.

### **Large herbivores increase spatiotemporal heterogeneity of ecosystems**

While large herbivores homogenize some variables over some (typically small) scales<sup>270,271</sup>, herbivore space use is spatiotemporally nonuniform<sup>272,273</sup> and impacts are thus heterogeneously distributed<sup>55,73,274–276</sup>. Gradients in geology, distance to water, tree cover, and other variables structure this variation<sup>153,264,275</sup>. Routinized feeding and movement patterns entrain nutrient cycling and substrate compaction<sup>74,277,278</sup>. Central-place behaviors create lasting nutrient hotspots<sup>75,163,225,279</sup>. Carcass decomposition causes local nutrient pulses<sup>226,280,281</sup>. Herbivory variegates fire extent and intensity<sup>182,198,282</sup> and also reduces plant species dominance and spatial aggregation<sup>47,95</sup>. Together, these spatiotemporally patchy impacts enhance many facets of heterogeneity at large scales relative to defaunated areas<sup>73,274,276,279</sup>.

### **Livestock do not functionally substitute for wild large-herbivore assemblages**

A dozen or so domesticated ungulates, mostly ruminants — and especially cattle, sheep and goats — displace wild large herbivores worldwide. Even multi-species livestock assemblages are functionally different and less diverse than native ones<sup>283,284</sup>. Livestock differ from their closest wild relatives in behavior, diet, and microbiome and parasite composition<sup>116,285,286</sup>. These differences are products of phylogeny, artificial selection, reduced ecological constraints (resource provision, protection from enemies), and management (herding, corralling)<sup>287</sup>. Livestock can thus attain exceptional densities<sup>288</sup>, a key predictor of impact<sup>54</sup>. Divergent effects of livestock and wild large herbivores have been documented in studies of plant and invertebrate communities<sup>289–293</sup>, primary productivity<sup>142</sup>, biotic invasions<sup>294</sup>,

fire regimes<sup>201,284</sup>, soil chemistry<sup>90</sup>, nutrient transport<sup>284</sup>, and methane emissions<sup>295</sup>. Functional discrepancies are greatest when native large-herbivore assemblages include influential species with no domestic analogue (e.g., elephants, hippos, marsupials, tortoises, arboreal primates)<sup>284,296–298</sup>.

Although livestock are not surrogates for wild large herbivores, the two can coexist and even harmonize<sup>299,300</sup>. Livestock can also provide closer or weaker approximations of native herbivory regimes. Long-term experiments that have independently manipulated wild and domesticated large herbivores affirm their differential impacts<sup>291,296,301</sup> but also emphasize that stocking rate and management practices determine the degree of difference<sup>176,302</sup>.

### **Knowledge gaps and frontiers**

The ability to articulate a list of qualitatively reliable global generalizations about the ecological impacts of large herbivores is a significant advance, even relative to the previous decade. Still, one could ask why the list is not longer or the generalizations more quantitatively precise. The intractability of large herbivores remains problematic, as it was 35 years ago<sup>1</sup>. But unlike then, there is no deficit of attention to large herbivores or of data for investigators to work with; today's challenges relate more to which types of data are being collected in which places, and limits on the depth of inferences that can be squeezed out of them. We briefly review several major impediments and important unresolved questions where they loom large.

Context dependence complicates the study of large herbivores at least as much as it does other areas of ecology<sup>303</sup>. But contingency has causes, and ecologists are increasingly able to evaluate them. In fact, several relationships underlying context-dependent variation in large-herbivore impacts have been known for years. At continental<sup>283</sup> to global<sup>4</sup> scales, large-herbivore biomass and diversity vary predictably with moisture (unimodal) and soil fertility (linear), which jointly regulate net primary production. In turn, productivity predicts the amount of plant biomass consumed by herbivores across terrestrial biomes<sup>19</sup>. These relationships, and the residual variance around them, highlight one major source of contingency in how large herbivores influence different environments. Although many grasslands and forests are similarly productive, forest biomass is far less available to large herbivores owing to its indigestibility (e.g., wood) and its height; thus, total herbivore consumption is roughly an order of magnitude higher in grasslands than in forests with equivalent primary productivity<sup>19,304</sup>. Proportional off-take is best predicted by plant turnover (ratio of production to biomass)<sup>304</sup>, which is low in forests and high in grasslands, such that a much greater fraction of primary production passes through herbivore guts in grasslands (e.g., 65% in the Serengeti<sup>23</sup> vs. 6.7% in tropical forests<sup>305</sup>). Furthermore, both turnover and plant-herbivore size ratio (which is also higher in grasslands) are theoretically predicted to increase the strength of top-down control<sup>306</sup>. However, the upshot of this logical chain — that herbivore impacts should be stronger in grasslands than in forests — is only partially supported by the available data. A cross-biome meta-analysis found stronger effects of herbivores on plant reproduction, abundance, biomass and diversity in grasslands (especially tropical ones), but statistical support for these differences was equivocal. Similarly, while many studies have

shown that climate, soil properties, landscape history and other factors mediate various large-herbivore impacts at local to global scales<sup>153,194–196,238,307,308</sup>, there is no unified framework for interpreting this variation. Unpacking environmental contingency is essential for forecasting responses to global change, but it will require experimentation in addition to macroecological and metabolic reasoning.

The difficulty of bridging scales of space, time, and biological organization is another challenge that is common to ecology but manifests in ways that are specific to large herbivores. Exclusion studies are indispensable for causal inference but are limited in size and duration (e.g., median of 48 m<sup>2</sup> in one meta-analysis<sup>47</sup>, 400 m<sup>2</sup> and 6 years in another<sup>49</sup>), making them prone to mischaracterize processes that occur over larger scales<sup>309–312</sup>. Use of exclusions for inferences about the effects of defaunation is problematic given both their scale and the fact that, especially in forests, fences exclude terrestrial folivores but not arboreal frugivores<sup>95,313</sup>. Conversely, observational, macroecological, and paleontological studies can reveal large-scale patterns but not their causes. We thus have rich but limited data at meters-to-hectare scales over 0–20 years, and at continental-to-global scales over >10,000 years; intermediate scales are less understood but are crucial for linking process to pattern<sup>303</sup>, as are the micro-scale molecular and biochemical mechanisms that ultimately underpin plant-herbivore interactions.

These rich datasets are also skewed both geographically and taxonomically. Research on large herbivores is concentrated in grassy ecosystems of a few countries in a few regions<sup>47,48</sup>, most of which have low large-herbivore diversity (Figure 4). In Africa, large-herbivore assemblages are diverse, but most studies occur in southern and eastern savannas with moderate rainfall<sup>53,54,314</sup>. Taxonomic bias towards ungulates (mainly ruminants) limits the ability to understand how large-herbivore impacts are regulated by body size vs. traits that are shared by ruminants but absent in other large herbivores — giant rodents<sup>315,316</sup>, macropods<sup>105</sup>, bears<sup>317</sup>, tortoises<sup>318</sup>, and birds<sup>319</sup>. These biases obstruct efforts to explain contingencies and bridge scales, and they foster the misleading perception that what occurs in intensively studied systems is ‘normal’, when in fact those systems may not be especially representative at higher levels (e.g., grazers in South Africa may mainly browse in Namibia or Mozambique)<sup>123,150</sup>. Geographic and taxonomic bias may also constrain scientific curiosity by imprinting junior researchers with preformed views on what research questions are interesting enough to pursue in the context of a given location or taxon. With that last risk in mind, we outline a set of still-unanswered questions that we find particularly interesting.

#### **What structures large-herbivore assemblages?**

Abundant indirect evidence indicates that large herbivores compete for food<sup>41,123,320–324</sup>, but direct evidence of competition is hard to obtain<sup>325,326</sup> (but see<sup>327</sup>). Facilitation among grazers is also widely hypothesized but equally hard to test<sup>41,299,328</sup>. Measuring the net effects of species interactions on population dynamics is even harder. Which traits confer competitive advantage under which conditions? If small-bodied species are competitively superior<sup>41</sup>, then why do large ones dominate communities (Figure 2) and global mammal

biomass<sup>66</sup>? How much niche differentiation along which axes is sufficient for stable coexistence<sup>67,123</sup>? Understanding and forecasting the impacts of large herbivores requires understanding what regulates their relative abundance and functional diversity.

The role of traits beyond size and diet type in shaping large-herbivore assemblages and impacts is unclear. Even for those traits, key gaps remain. Body size affects, and is thus difficult to isolate from, local biomass and diet composition (Figure 2). Diets have been characterized coarsely, often categorically, in ways that predict correspondingly coarse-grained responses<sup>54</sup> but eclipse nuance that is surely important for predicting other impacts. Traits such as water requirements, thermoregulatory strategy, and social behavior, which are ecologically central in the context of anthropogenic global change, have received comparatively little attention<sup>329</sup>.

#### **How do large herbivores affect carbon, water, and nutrient cycles?**

There is great interest and great uncertainty about the role of large herbivores in carbon cycling and climate regulation<sup>3,44,49,330–337</sup>. Despite hope that large herbivores can be part of nature-based solutions for enhancing carbon uptake and storage<sup>338–340</sup>, their effects on net ecosystem exchange can be positive, negative, or neutral<sup>49,341–343</sup>. Case studies neatly illustrate this point: increased wildebeest abundance flipped one savanna from a source to a sink of woody biomass carbon<sup>214</sup>, whereas increased elephant abundance flipped another savanna in the opposite direction<sup>344</sup>. Accounting is difficult because large herbivores affect net carbon fluxes through many pathways that can offset each other: biomass removal; shifts in productivity and plant allocation to roots vs. shoots; and alteration of vegetation type, fire regime, albedo, litter inputs, soil C fractions, microbial biomass and respiration, substrate compaction, subsurface temperatures, and methane production<sup>214,295,319,344–350</sup>. Modern remote sensing facilitates large-scale measurement of large-herbivore effects on aboveground carbon<sup>276</sup>, but large herbivores also affect belowground stocks in variable ways. The latter are harder to quantify at scale but crucial to understand, because they comprise the majority of carbon stored in many systems where large herbivores are dominant consumers, such as grasslands<sup>90,91,351–353</sup>.

Although water regulates the distribution and abundance of large herbivores and *vice versa*, hydrology remains poorly incorporated in the study of large herbivores<sup>273,354–357</sup>. A standardized global survey found strong but intricately context-dependent effects of grazing intensity on soil water-holding capacity and porosity<sup>55</sup>. Transport of terrestrial carbon into aquatic systems by large herbivores and subsequent decomposition under anaerobic conditions can elevate CO<sub>2</sub> and methane emissions from surface waters, thereby altering ecosystem carbon balance<sup>358</sup>. Changing precipitation and surface-water regimes, along with artificial water supply by managers, may transform large-herbivore assemblages, because species vary widely in their water requirements<sup>273,354,359</sup>. These uncertainties underscore the need for further integration of earth science and large-herbivore ecology<sup>3</sup>.

The role of large herbivores in nutrient cycling has received relatively more attention but remains clouded by uncertainty.

Notably, while it is clear large herbivores are long-distance vectors of organic and inorganic nutrients, and the composition and distribution of those inputs are quantified in a growing number of studies, evidence on the net impacts of that transport is weak. Which ecosystem functions are impaired, by how much, when lateral nutrient flow is truncated by defaunation<sup>42</sup>? Do long-ranging large herbivores stabilize communities by coupling distinct energy channels, as theoretically predicted<sup>360</sup>? How does body size regulate the role of large herbivores in nutrient cycling<sup>361</sup>? Body size affects ratios of nitrogen, phosphorus, and minerals to an extent that can alter plant productivity and community composition, but the exact form and determinants of this relationship are unclear<sup>230,231,362,363</sup>. Research in this area has focused mainly on nitrogen and feces, and less on other elements, urine, and carcasses<sup>364</sup>.

Similarly, the impacts of seed dispersal by large herbivores are heavily studied, long debated, and extremely difficult to measure<sup>365,366</sup>. Simulation models suggest that dispersal of large-seeded, dense-wooded trees by large herbivores enhances carbon storage<sup>341,342,367–369</sup>, but these models rely on strong, unverified assumptions about how strictly trees depend on animal dispersal. Notably, putatively megafauna-dependent plants in Neotropical forests have persisted for millennia without the megaherbivores extinguished during the Pleistocene, in part by developing novel adaptations and mutualisms<sup>370–372</sup>. Experiments often detect little effect of large herbivores on forests<sup>373–376</sup>. Observational studies of intact and defaunated forests more reliably detect effects but struggle with causal attribution<sup>313</sup>. Seed dispersal is largely ignored in grassy biomes<sup>377,378</sup>, yet savanna herbivore dung germinates many seedlings, and savanna grasses have traits suggestive of alternative megafaunal and abiotic dispersal syndromes<sup>379,380</sup>.

#### **Does herbivore-associated microbiota affect ecosystem processes?**

The study of how microbes mediate herbivore–environment interactions is nascent. Herbivore microbiomes are seeded and shaped by the environment; in turn, large herbivores can alter environmental microbiomes via direct (egestion of microbes) and indirect (habitat modification) pathways<sup>381,382</sup>. Egestion of gut microbes has lately been recognized as relevant to ecosystem functioning and may be influential in dense herbivore assemblages. Gut microbiomes differ from ambient ones given the differences between guts and external environments, but when those differences are relaxed (e.g., in water), some microbes can function outside the host and affect biogeochemistry. Hippos can push freshwater systems to anoxia by importing terrestrial matter in feces, turning pools into extensions of the gut where some bacteria continue biodegradation and production of CH<sub>4</sub>, N<sub>2</sub>O, and H<sub>2</sub>S<sup>358,383</sup>. Dead herbivores also export microbes to the environment, including some of those that decompose carcasses<sup>384–386</sup>. Different herbivores host distinct microbiomes, which covary with phylogeny and diet, suggesting non-redundancy of species' effects on microbially mediated functions<sup>285</sup>. The 'metamicrobiome'<sup>382,383</sup> is a frontier that may be key to understanding herbivore impacts, just as gut microbiomes are key to understanding herbivore physiology<sup>387,388</sup>. But fully incorporating microbial dynamics exacerbates the already-daunting hurdles of complexity and scale and requires

attention to molecular mechanisms that lie beyond the traditional remit of ecology.

#### **Do large herbivores affect ecosystem distribution at large scales?**

Herbivore exclusion increases tree cover, and late-Pleistocene extinctions preceded shifts in fire regimes and plant communities, both of which suggest that large herbivores help to maintain the distribution of ecosystems and ecotones within abiotic constraints<sup>213,389,390</sup>. The extent to which large herbivores trigger shifts in ecosystem distribution and alternative stable states (e.g., forest to grassland, steppe to tundra) is unclear<sup>391–394</sup>. In the Serengeti, elephants maintained grasslands but could not cause woodland to grassland transition without fire<sup>213</sup>, while rising wildebeest abundance reduced fire and increased tree density but did not cause forestation<sup>214</sup>. Trampling of vegetation by forest elephants at forest–savanna boundaries created natural fire breaks that stabilized the ecotone<sup>395</sup>. While large herbivores alone therefore seem more likely to stabilize than transform ecosystems, interactions between large herbivores and fire or climate — which can be decoupled by human activity — are potent and difficult to predict.

#### **Evolutionary and eco-evolutionary dynamics**

Amazingly few studies have quantified selection or evolutionary response in large herbivore–plant interactions<sup>396–399</sup>, in sharp contrast to the study of insect–plant interactions<sup>400</sup>. Current knowledge is based on inference from modern ecological interactions, comparative floristic analysis, and sparse macroevolutionary data. For example, spines deter browsers<sup>401</sup>, plants protected from browsers have shorter spines<sup>82,192</sup>, plants on islands without large herbivores have fewer spines<sup>402</sup>, and phylogenies show that spines evolved repeatedly in concert with the diversification of bovids<sup>186</sup>. Spinescence undoubtedly evolves in response to selection by large herbivores. Yet, definitive evidence is hard to pin down. Plant response to herbivory depends on tolerance mechanisms and plant–plant interactions in addition to resistance mechanisms such as spines, meaning deterring browsers does not necessarily increase fitness. Spines are phenotypically plastic<sup>82</sup>, meaning that observed associations between herbivory regime and spine phenotype do not necessarily indicate heritable variation. Persistence of 'Pleistocene anachronisms', such as spiny Neotropical trees in forests with few or no browsers<sup>11</sup>, highlights that modern associations are unreliable indicators of past or future evolutionary processes<sup>403</sup>. And while the co-diversification of spiny plants and bovids in Africa<sup>186</sup> is compelling, it is not immediately obvious why Miocene bovids would select more strongly for spines than Oligocene browsers<sup>404</sup>. The point is that even this exceptionally convincing evolutionary inference is potentially fallible; other evolutionary hypotheses have far less support.

The approaches of modern microevolutionary biology can be applied to large herbivore–plant interactions: common-garden experiments to establish heritability<sup>405</sup>, quantitative measurements of selection, and elucidation of genes and gene-expression patterns underlying traits under selection by large herbivores. Development of large herbivore–plant model systems with advanced genomic resources would deepen the understanding of modern interactions and eco-evolutionary feedbacks, along with the ability to forecast rapidly evolving dynamics in the Anthropocene<sup>371,406–408</sup>.

### How do predators regulate large-herbivore impacts?

Different predation regimes are often associated with different vegetation, but it is hard to establish that this is the result of a trophic cascade — and, if so, whether the cascade is mediated by herbivore behavior, density, or both<sup>252,255</sup>. Most research in this area rests on correlative data, but manipulative experiments provide the strongest evidence both for<sup>77,264–266</sup> and against<sup>252,268,269</sup> trophic cascades. The gold standard<sup>409</sup> requires showing that predation or risk affects herbivores, that herbivores affect plants, and that predators indirectly affect plants. Yet, few studies independently manipulate predation and herbivory<sup>264,266</sup>. To this end, cheap devices for experimentally simulating risk<sup>260,263,410</sup> can be combined with exclosures, and data on animal movement and diet can help to constrain other uncertainties<sup>266</sup>.

### How well does herbivore diet predict impacts?

The cumulative biomass of grazers and browsers predicts the strength of their effects on grasses and trees<sup>54</sup> — but herbivore diets also differ at finer grains<sup>123,411,412</sup>. What explains those subtler distinctions, and to what extent do they predict impacts of large herbivores on plant biodiversity? Variation in herbivore diets is correlated with both herbivore and plant traits<sup>112,114</sup>, but more work is needed to understand how those associations emerge. In particular, effects of chemical defenses on large-herbivore diets are little known but surely important<sup>127,413,414</sup>. Phenolic compounds are known to influence large herbivores' food choices and nutrition<sup>415–418</sup>, but a vast array of other metabolites remains unstudied. Advances in metabolomics<sup>419</sup> and genomics<sup>400</sup> can unblock research on how plant toxins mediate diet and how gut microbiomes mediate toxicity<sup>387</sup>.

Will a deeper understanding of diet in turn facilitate predictions about herbivore impacts on plants? Herbivore preference alone predicts a limited amount of variance in plant response to large-herbivore exclusion (Figure 5D). Differences in plant tolerance and effects of large herbivores on plant–plant interactions contribute to this unexplained variance<sup>190,192</sup>. Preliminary data from one system show that herbivore food preference and plant traits related to tolerance or competitive ability can together predict plant species' responses to herbivore exclusion better than models based on herbivore consumption alone (Figure 5D).

Because body size and diet type generally differentiate herbivore species' ecological impacts, and because sympatric species universally differ in size and diet (Figures 2 and 5), species are not functionally redundant in a strict sense. Yet, redundancy is theorized to be widespread and important in governing robustness to species loss<sup>420</sup>, and it is a matter of degree. While no two large herbivores are ecologically equivalent, the realized extent of functional redundancy (or its inverse, complementarity) is uncertain. Small large herbivores cannot compensate for big ones, nor can grazers replace browsers. But can plains zebra (300 kg) compensate for the extinction of endangered Grevy's zebra (400 kg) — sympatric species that both eat >95% grass but differ in dietary species composition, water dependence, and space use<sup>116,421</sup>? Any difference in net impact might be undetectable and practically irrelevant. Similarly, niche complementarity is thought to explain positive biodiversity–ecosystem function relationships. How do the impacts of large-herbivore assemblages depend on their species richness?

These questions are relevant both to forecasting consequences of extinction and to understanding the extent to which species can serve as proxies for one another. This concept of surrogacy is invoked not just in relation to the substitutability of wildlife and livestock, but also increasingly in the context of rewilding scenarios that propose to reproduce prehistoric herbivory regimes using extant species in lieu of extinct ones<sup>30,38,422</sup>. Studies that have tried to address the last question by reconstructing multidimensional functional-trait spaces suggest that introduced ungulates recover a substantial fraction of Pleistocene ecosystem functions<sup>38</sup>, but it is unclear how closely trait spaces map onto realized impacts.

### Synthesis

*“The key to prediction and understanding lies in the elucidation of mechanisms underlying observed patterns.”* — Simon Levin<sup>423</sup>

Recent work on the ecological impacts of large herbivores has built on longstanding conceptual foundations to solidify and refine a set of robust generalities while simultaneously advancing on multiple new fronts. The catalyst for these advances has not been the birth of new paradigms or formal theory, but rather enhanced power to discern empirical patterns and the scales at which they hold. The increasing scale and resolution of remote sensing<sup>424</sup>, use of camera traps<sup>425</sup>, innovation and miniaturization of telemetry devices<sup>426</sup>, fusion of field and laboratory methods<sup>285</sup> and development of big data repositories have all synergized with time-tested observational and experimental methods to enable progress (Figure 3). Despite this progress, the challenges of complexity, scale and contingency prevent answers to many classic questions<sup>303,423</sup>. The scope of unsolved problems reveals a mismatch between the state of knowledge and ecologists' aspiration to predict and mitigate global change<sup>29,32,40,427,428</sup>. We identify two problems that underlie many of the specific uncertainties reviewed in the preceding section.

### Weak inference about process

Mechanistic insight is not required for generalization, but it is for understanding and predictive power<sup>423</sup>. Ecological phenomena have layers of mechanisms at different levels of organization. Observational and macro-data are invaluable but cannot establish cause–effect relationships. Exclosures and other experiments can link cause to effect, but most are mechanistic only to the first order: they reveal the cause of an outcome, but not the processes that produced it, nor how and why the outcome depends on environmental conditions and experimental scale. Piercing deeper layers of mechanism — e.g., whether direct effects resulted from consumption or trampling, which indirect pathways also contributed — requires additional experiments and data.

One view is that mechanistic generalization is hopeless in the face of contingency, and that ecologists should focus on large-scale patterns and ignore “messy details”<sup>303</sup>. Another view is that multi-method research across scales is synergistically clarifying<sup>429</sup>. Some work reviewed here affirms the latter take. For example, early intuition that large herbivores might enhance grassland plant diversity at high (but not low) primary productivity by alleviating competition for light<sup>430</sup> was conceptually formalized and bolstered by site-specific work<sup>16,193</sup>. Syntheses of exclosure data over ever-larger scales later confirmed the



generality of that context-dependent effect and implicated light competition as the cause<sup>107,194,431</sup>. Targeted experiments eventually confirmed that mechanism<sup>195</sup>. In this case, the dynamic interplay of natural history, theory, and empiricism at multiple scales resolved ‘messy’ contingency into mechanistic rules.

#### **Weak understanding of species-specific impacts**

One type of mechanistic uncertainty particularly thwarts understanding and prediction of Anthropocene dynamics. Most experimental and macro-scale research measures effects of large-herbivore assemblages or guilds — often quantifying differences between an intact fauna and no large fauna at all. In contrast, defaunation and restoration are typically piecemeal, with populations declining at uneven rates or being reintroduced one at a time. Prevailing study designs are incongruent with those scenarios. It is usually impossible to manipulate just one large-herbivore species, or to exclude small species without excluding large ones; selective exclosures remove nested subsets of species. Also, exclosures are designed to remove all individuals, not to simulate population decline.

Inability to isolate the effects of individual species prevents a process-based accounting of net assemblage-level impacts, which emerge from species-specific effects that differ in magnitude or even direction. It also limits ecologists’ ability to answer practical questions that arise in real-world management settings. Conservation and restoration emphasize the survival of iconic species but increasingly aim to incorporate ecological processes. How are those two goals linked? How well or poorly does species conservation align with total biodiversity, carbon sequestration, and other ecosystem services? When should a species be considered functionally extinct<sup>371,432</sup> or overabundant<sup>389</sup>? Does the order of species reintroductions matter in restoration, for example by impeding or aiding reestablishment of other species? Can managers harness large-herbivore functional ecology to predict and mitigate human–wildlife conflict<sup>433,434</sup>?

#### **Outlook**

Ecology is not unique among sciences in confronting complexity, contingency, problems of scale, emergent properties, and an urgency to translate basic research into applications. For some reason, physics is the standard measuring stick for ecology’s insecurities<sup>303,435,436</sup>. Comparison to other branches of biology seems more apt, but there is a cultural difference between fields — namely that ecology has been far less patient with bottom-up (‘reductionist’) empirical progress than molecular, cell, or developmental biology. Whatever its limitations, reductionism has propelled the greatest advances in biology over the last century. With technology releasing ecologists from old empirical constraints, it is getting easier to envision bridging scales via a renewed commitment to process-based inquiry. We offer some suggestions.

#### **Developing and sustaining model systems**

Model systems (e.g., yeast, *Drosophila*, *Arabidopsis*) are amenable to research, which attracts investigators, which further unlocks the system and often yields generalizable discoveries. Research on the effects of large herbivores has model systems: deer, Yellowstone, Serengeti, Kruger, a few multi-decadal experiments (Figure 4). Continued investment in these systems will pay dividends and need not undermine the goal of reducing

geographic and taxonomic bias in research effort: insights from existing model systems facilitate the establishment of new ones.

#### **Relying less on categories**

To categorize is human. However, as discussed above in relation to defining ‘large herbivores’ and feeding guilds, discretizing continuous variables for analysis discards and obscures information, sometimes to the point of misrepresentation. Ecologists can embrace the heuristic value of categories for conceptualization and efficient communication while also estimating and analyzing real quantities (body mass, proportional grass consumption) whenever possible.

#### **Relentlessly pursuing mechanisms**

Process-based understanding requires multiple strategies: conducting follow-up experiments and experiments-within-experiments to isolate candidate mechanisms and distinguish direct vs. indirect effects, collecting data on organismal and environmental covariates and building rigorously parameterized models. This entails a shift in focus away from testing null hypotheses of ‘no effect’ towards explaining how effects emerge. Similarly, attacking contingency entails a shift from showing that effects vary (they do!) towards explicitly testing factors that regulate effect size and direction. Climate change is altering many sources of contingency, which creates opportunities to evaluate those factors and also helps justify the effort required to do so.

#### **Devising next-generation field experiments**

Beyond maintaining existing long-term exclosures, which continue to yield new insights after decades, the conventional model can be expanded with innovations to address the limitations discussed above. Concerns about replication lead researchers to build many little, individually fenced plots, but one mega-exclosure (e.g., Kruger’s >250-ha Hlangwini and Nwaswitshumbe sites<sup>141</sup>) could address questions of scalability without sacrificing rigor. Intermittently opening and closing fences, or building them as herbivore deterrents rather than removals, could test effects of density reduction. Enclosing one or two individual large herbivores in hectare-scale exclosures could test species-specific effects at realistic total biomass densities, similar to the controlled cattle grazing in a Kenyan experiment<sup>176</sup>. Planned obsolescence — systematic removal of replicated exclosures at intervals — could be used to test hypotheses about resilience and alternative stable states<sup>104,106</sup>.

#### **Gathering contextual data in experimental studies**

Basic data such as herbivore densities are needed to interpret exclosure results but are often not collected<sup>47,54</sup>. Combining manipulation with modern monitoring techniques can be especially potent. These include measurement of plant traits and soil chemistry<sup>437</sup>, hyperspectral imaging and LiDAR<sup>276</sup>, subsurface imaging<sup>351</sup>, GPS telemetry<sup>438</sup>, DNA metabarcoding<sup>266</sup>, metabolomics and transcriptomics<sup>439</sup>, flux towers, and machine-learning algorithms to mine these and a growing array of other data that can be continuously logged in the field (Figures 3 and 5). Long-term monitoring of individual plants across ontogeny using this slate of tools would be informative.

#### **Capitalizing on fortuitous large-scale events**

Environmental interventions are often revelatory<sup>440</sup>. Conservation translocations of large herbivores are increasingly frequent<sup>29,428,441</sup> and represent species-specific experiments at otherwise impossible scales, as do population crashes and

culls<sup>327</sup>. Wildlife ranching is a business<sup>442</sup> that enables planned experiments with non-domestic large-herbivore species that would be unthinkable in protected areas. The scientific interest in these opportunities may often align with the interests of other stakeholders (e.g., shared interest in why translocations succeed or fail<sup>441</sup>).

### Bottom-up mechanistic modeling

While the aforementioned set of approaches will deepen basic understanding and crystallize new insights, they are not a recipe for predictive power. Yet, they might be essential ingredients. We do not foresee extremely accurate and precise forecasts of the impacts of perturbations to large-herbivore communities. But we can envision a common quantitative framework based on species' traits and interactions that provides actionable guidance to those attempting to manage and conserve large herbivores and their habitats in the Anthropocene<sup>51,283,443,444</sup>.

### ACKNOWLEDGMENTS

We thank Matthew Luskin, Elizabeth le Roux, and Mauro Galetti for insightful comments on the manuscript. Johan Pansu created Figure 2E. We acknowledge research support as follows. R.M.P.: US National Science Foundation (NSF) IOS-1656527 and DEB-2225088, Cameron Schrier and Greg Carr foundations, and High Meadows Environmental Institute. J.O.A.: NSF Graduate Research Fellowship. J.R.G.: NSF DEB-1930763, DEB-2018405, DEB-2132265. R.A.L.: NSF IOS-1656642. A.L.S. and C.L.D.: NSF DEB-1354053, DEB-1354062, DEB-1753727, DEB-2103884.

### DECLARATION OF INTERESTS

R.M.P. is a member of the *Current Biology* advisory board. The remaining authors declare no competing interests.

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