Review

Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas

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Herbivores are regulated by predation under certain environmental conditions, whereas under others they are limited by forage abundance and nutritional quality. Whether top-down or bottom-up regulation prevails depends both on abiotic constraints on forage availability and body size, because size simultaneously affects the risk of predation of herbivores and their nutritional demands. Consequently, ecosystems composed of similar species can have different dynamics if they differ in resource supply. Here, we use large herbivore assemblages in African savanna ecosystems to develop a framework that connects environmental gradients and disturbance patterns with body size and trophic structure. This framework provides a model for understanding the functioning and diversity of ecosystems in general, and unifies how top-down and bottom-up mechanisms depend on common underlying environmental gradients.

Herbivore regulation and the implications of body size

The global decline of large herbivores, owing to human-induced land-use changes, raises concerns for the long-term conservation of species whose ranges are being reduced to a few protected areas [1]. The local extirpation of large herbivores has consequences for entire ecosystems, because of their role in maintaining the diversity of predators and primary producers [2]. Understanding herbivore regulation across resource gradients, such as rainfall, is important for the long-term management and conservation of ecosystems, especially if shifts in global climate result in a mismatch between the location of protected areas and the preferred niche of a species. Here, we investigate how resource gradients simultaneously influence top-down and bottom-up processes in ecosystems, using the large herbivore community of African savannas as a generalized example. The model could also prove useful in understanding the relation between disturbance, resource gradients and trophic structure in other ecosystems.

Classic food chains represent relationships between trophic levels as linear bottom-up or top-down processes: abiotic factors such as rain determine primary production, which is consumed by herbivores, which are themselves in turn consumed by carnivores. The abundance of herbivores can therefore be controlled through top-down mechanisms, such as predation [3–5], or through bottom-up constraints on primary production, such as soil fertility (Figure 1) [6–9].

Trophic cascades in linear models of herbivore regulation (Figure 1) involve the knock-on effects of predation expressed at alternate trophic levels [10]. In the classic example, predators limit the abundance of herbivores, which releases grazing pressure on plants (the ‘green world’ hypothesis) [11]. Here, the abundance of vegetation is determined largely by the availability of abiotic resources as herbivores are regulated by predators [5,12].

Previous research has elucidated the complexity of trophic interactions by breaking each trophic level into more fundamental components (Figure 1). Specifically, the roles of abiotic factors, disturbances, quality and quantity of primary production, and the effect of body size have each been shown to influence independently the distribution and abundance of herbivores. Here, we show how common underlying environmental gradients influence both top-down and bottom-up regulation simultaneously. Differences in the relative accessibility of limiting resources can cause ecosystems with similar species to have different regulatory mechanisms. In addition, the body sizes of herbivores determine both their susceptibility to predators and their resource requirements. We show how this generalized model accounts for observed differences in the trophic functioning of the large herbivore community in savanna sites across Africa. Although humans evolved in African savannas and historically affected herbivores through hunting and fire, substantial land-use changes and increasing human populations have put unnatural demands on these systems, creating a need for a better understanding of ecosystem dynamics.

Predation: not all herbivores are affected equally

The simple food-chain view of predator–prey interactions (Figure 1) ignores the fact that not all carnivores can consume all species of herbivore, and not all herbivores are equally susceptible to all carnivores. Large prey, such as buffalo (*Syncerus caffer*), are difficult to capture and are only consumed by the largest predators, such as lion. Whereas small predators can only consume small prey, large predators might consume both large and small prey (Figure 2a) [13,14]. Recent work proposes that predation has a greater impact on regulating a population of small

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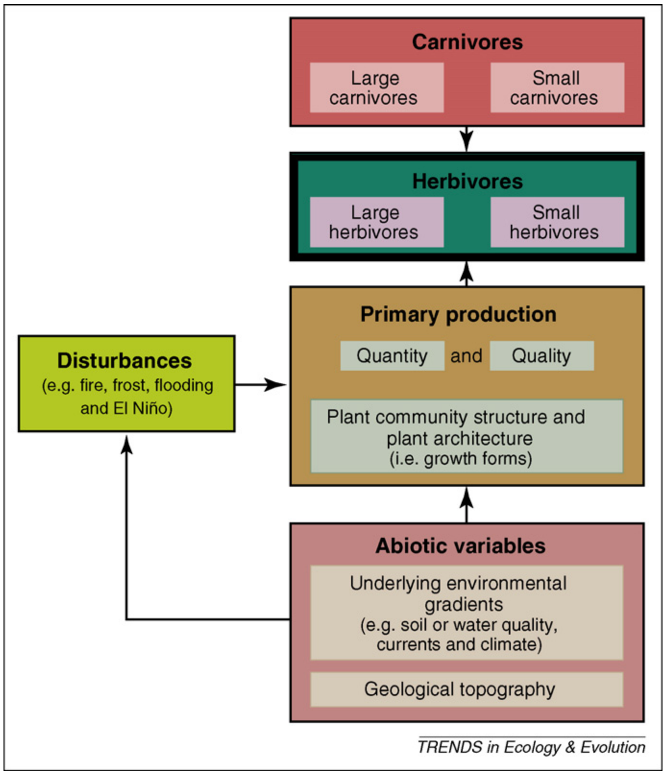

Figure 1. Factors responsible for regulating herbivore abundances across ecosystems. In this classic food chain approach, the abundance of herbivores is regulated by top-down processes, such as predation, and by bottom-up processes through primary production (arrows indicate the direction of influence). Herbivores (similar to carnivores) are considered as a single unit, despite showing strong functional divergences based on body size. Primary production in this framework is a general term that fails to distinguish the differences between the quality, quantity and structure of a plant community.

body-sized herbivores (e.g. oribi, *Ourebia ourebi*) when the prey base of small predators is nested within that of large predators, as this exposes smaller herbivores to more enemies (Figure 2a) [15]. Conversely, if predators specialize on particular size classes of prey (i.e. they partition the prey base), predation pressure is expected to be relatively even across all body sizes, until the prey become too large (Figure 2b).

Therefore, the degree of regulation of herbivore populations by predation depends on both the relative body size of predators and prey, and the way in which the available prey base is partitioned by carnivores of different sizes (Figure 3a). Furthermore, the largest predators (lion) are also the most dominant and kill smaller predators (cheetah or hyena), or chase them away from their prey (Figure 3a) [16,17].

Recent studies provide evidence that both size-nested and size-partitioned predation occur (Figure 3b). In the Serengeti system (Tanzania), large prey such as buffalo (450 kg) generally escape predation except from cooperatively hunting lions, whereas oribi (18 kg) are eaten by many species [3,18], illustrating size-nested predation (Figure 3b). Studies in Kruger Park, Hluhluwe-iMfolozi, and Phinda (South Africa) provide evidence for size-partitioned predation, where large predators, such as lion, concentrate on prey of approximately their own body mass [4,19] (but see Ref. [15]). Only prey species with a body mass >1000 kg, such as hippo (*Hippopotamus amphibius*) and white rhino (*Ceratotherium simum*), tend to escape predator regulation in Kruger, whereas prey species heavier than 150 kg, such as buffalo, escape predator regulation in Serengeti. The largest herbivores, such as elephant (*Loxodonta africana*), are too big to be captured irrespective of whether predation is size nested or size partitioned [20,21] (with the exception of juveniles).

In summary, top-down processes are modified by the way in which carnivores partition their food niches and the degree to which larger carnivores dominate smaller carnivores. Explanations as to why there are differences in the mechanism of niche partitioning of predators in otherwise similar food chains can be found in the type of vegetation that supports herbivores and the disturbance regime, which we explore here.

Forage quality and abundance: not all that is green is edible

Geographical processes involving erosion of parent material, and rainfall, determine key environmental gradients, such as soil fertility and water availability [22,23], which influence vegetation structure [7,24,25]. Plant structure, in turn, determines the quality and quantity of digestible material available to herbivores (Figure 4a) [9,26–30]. Primary production varies along environmental gradients [31] and regulates herbivore populations through classic bottom-up processes of resource limitation (Figure 4a) [8,32–34]. The quantity of primary production increases with rainfall and soil fertility, so that in the absence of herbivory or fire, the largest standing biomass is found in fertile areas with unlimited moisture, but declines when either water or soil nutrients become limiting (Figure 4b) [7,29,35]. Under high rainfall conditions, plants invest more resources in structural support and protection against herbivory (e.g. stems, lignified tissues, secondary compounds and mechanical defenses [35,36]). As a result, the digestible quality of primary production is inversely related to rainfall (Figure 4b), so that the energy and nutrients per unit biomass that is extractable by herbivores declines as conditions become wetter [37].

Herbivory provides the most direct access to consumable energy and has evolved multiple times in many unrelated taxa (e.g. molluscs, birds, mammals, insects, reptiles, fish and marsupials) from both carnivorous and detrivorous ancestors [38]. To digest cellulose, ungulates use a symbiotic fermentation process in the rumen or cecum that is relatively time-consuming and requires a specialized gastrointestinal tract. Small ungulates such as oribi and Thomson's gazelle (*Gazella thomsoni*) have smaller gastrointestinal systems and, therefore, shorter ingesta retention times [20,21,39], which means they cannot process coarse vegetation. Furthermore, small endotherms have a higher energy expenditure per unit mass. These two factors mean that small herbivores have to select the most nutritious, highest energy forage (Figure 4c) [26,28,40,41]. Larger herbivores are relatively unconstrained by the size of their gastrointestinal tract and have longer retention times; thus, they can extract enough energy from poorer quality food, providing there is sufficient quantity [40,42] (Figure 4c).

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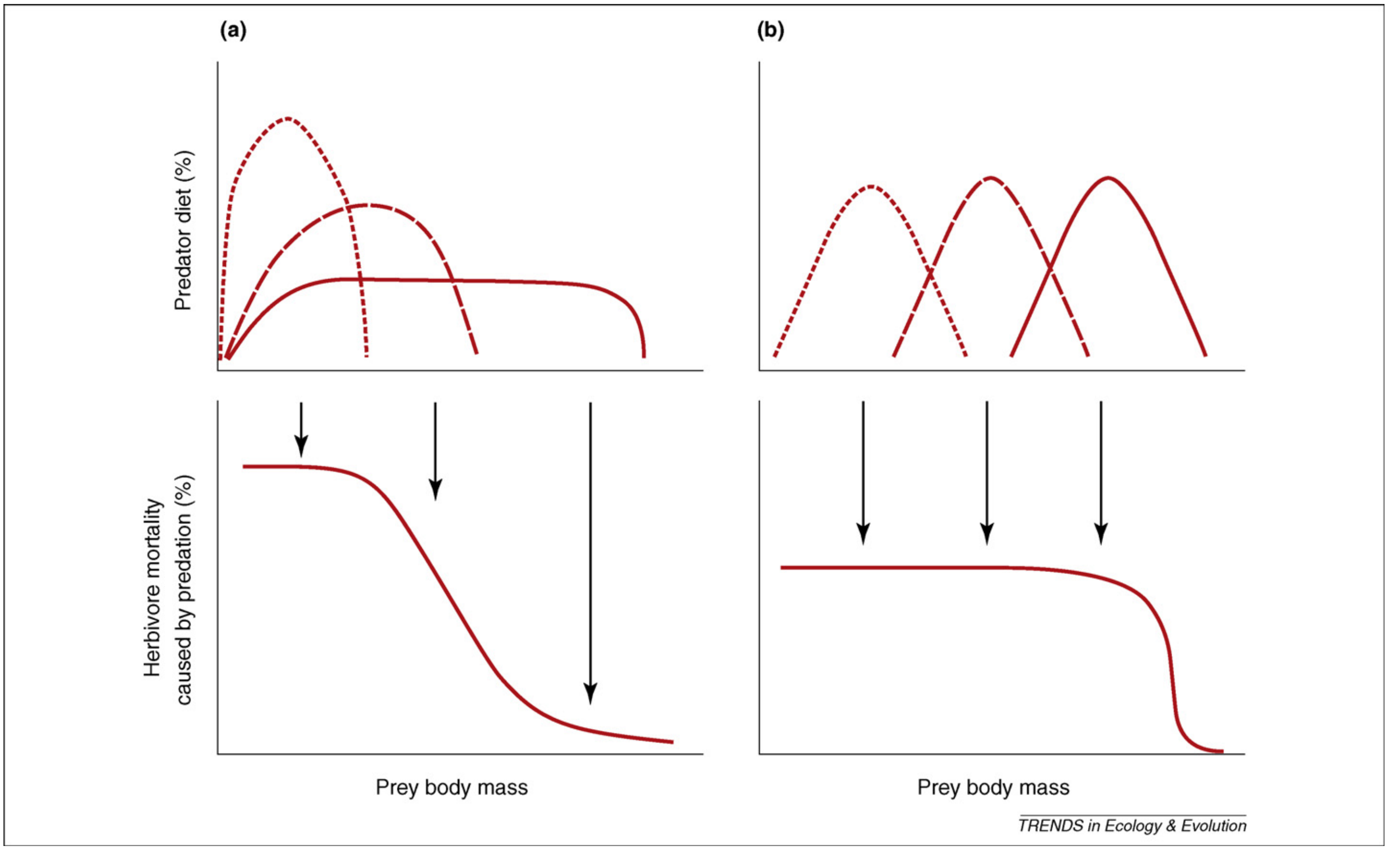

Figure 2. The relationship between the degree of herbivore mortality owing to predation and the diet selection of the predators. **(a)** If large predators (solid line in upper panel) are opportunists and consume prey of all sizes, whereas small predators (dotted line) only kill small prey, then the prey base of small predators is nested within that of large predators (size-nested predation). Medium-sized predators are indicated by the dashed line. The cumulative mortality on small prey is greater than on large prey (lower panel) because they are exposed to more predators. **(b)** If predators are selective, and only consume prey of a specific size class (size-partitioned predation), then large predators do not supplement their diet with small prey. When predation is size-partitioned as opposed to size-nested, the cumulative mortality owing to predation on small prey is less, whereas large prey are killed more often.

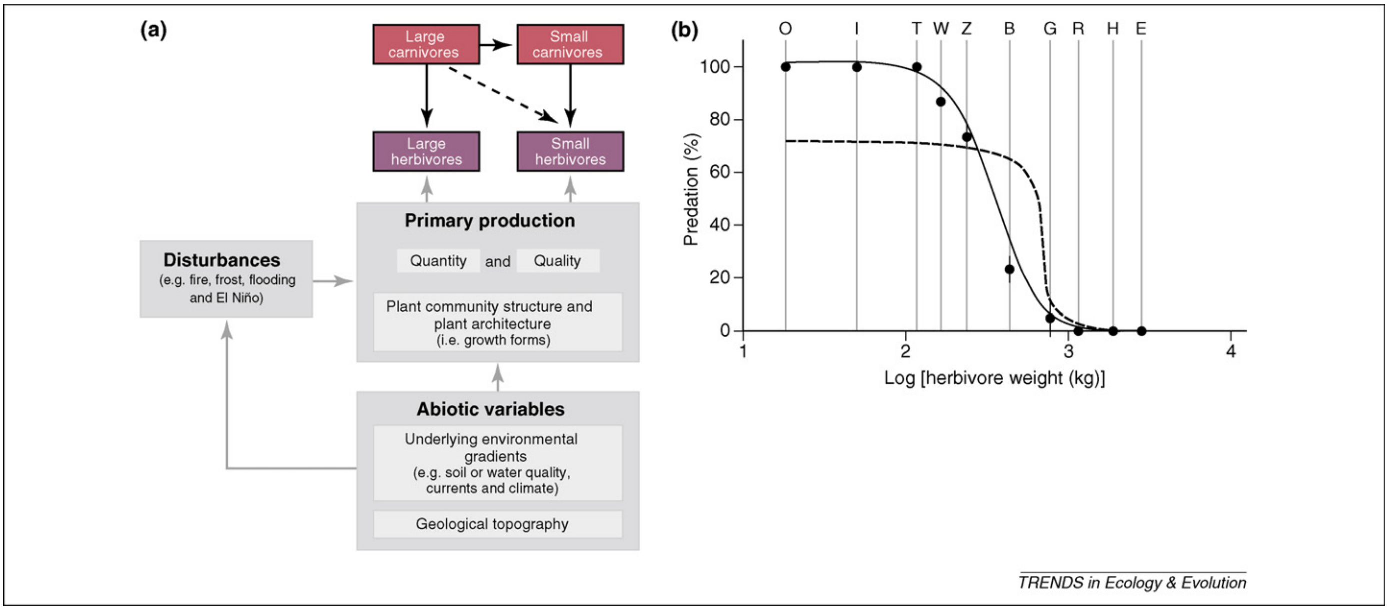

Figure 3. The relative importance of predation in regulating herbivore populations depends on the body size of predators and their degree of specialization for certain prey. **(a)** Following from Figure 1, if large carnivores only eat large prey, and small carnivores only eat small prey (solid vertical arrows), the prey base is partitioned. If large carnivores eat both large and small prey (solid and dashed vertical arrows), the prey base of smaller carnivores is nested within that of larger carnivores. Large carnivores dominate small carnivores and reduce their efficiency (solid horizontal arrows). **(b)** When predation is nested, small prey are exposed to more predator species and become increasingly predator regulated, as in the Serengeti example (solid line). When predation is partitioned, large prey suffer greater predation than do small prey because large predators do not supplement their diet with small prey, as in the Kruger example (dashed line). Data for Serengeti and Kruger from Refs [3,4,64]. Abbreviations: B, African buffalo; E, elephant; G, giraffe; H, hippo; I, impala; O, oribi; R, black rhino; T, topi; W, resident wildebeest; Z, resident zebra.

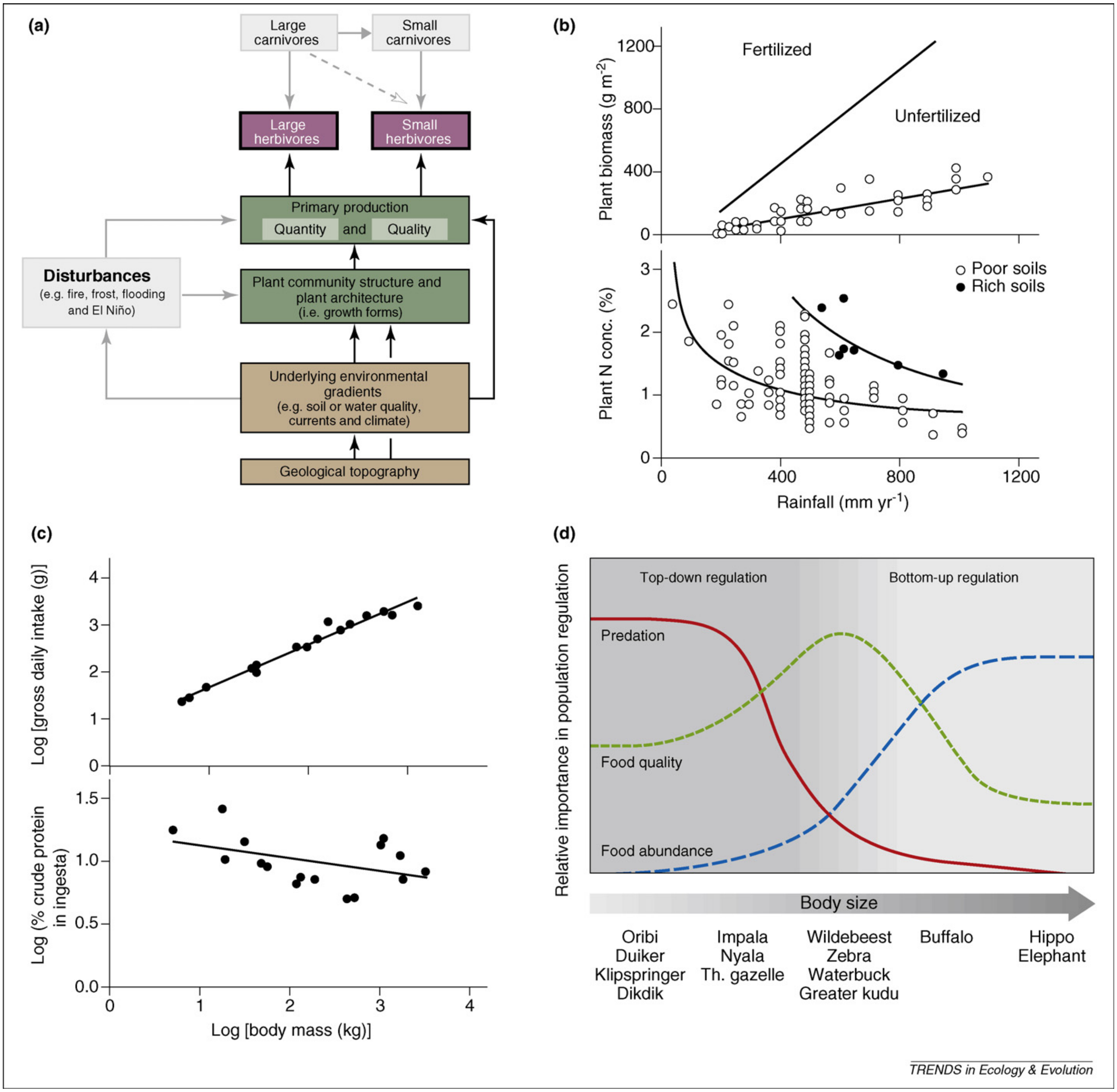

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Figure 4. Regulation of large versus small herbivores by the quality versus quantity of primary production. **(a)** Physical and environmental gradients have direct and indirect effects (i.e. between non-adjacent levels) on the plant community structure and on the quality and quantity of primary production. **(b)** For example, the quantity of plant biomass is positively related to increasing rainfall and soil fertility, whereas the digestible quality of the plant declines with increasing rainfall. **(c)** Large herbivores consume greater quantities of lower quality food, whereas small herbivores consume less food of higher quality because they are constrained by their high metabolism and limited digestive capacity. **(d)** Therefore, large herbivores, such as elephant, tend to be regulated by food abundance (dashed blue line), whereas smaller herbivores, such as wildebeest, are regulated by food quality (dotted green line). The smallest herbivores, such as oribi, are mainly predator regulated (solid red line). Reproduced, with permission, from Refs [35] (b) and [21] (c).

In summary, plant quality and biomass are determined by both environmental gradients and plant growth form (Figure 4a). These affect small and large herbivores differently owing to differing metabolic constraints. The result is that smaller herbivore populations are nutritionally limited by the quality of forage, whereas populations of larger grazers are limited by the quantity of food (Figure 4d).

The role of disturbances, facilitation and ecosystem engineers

Sudden shifts in primary production caused by abiotic disturbances such as fire, or marked changes in consumption rates (either herbivory, predation or infection) potentially rearrange the dynamics of an ecosystem either temporarily or semi-permanently into a new state [43,44]. Given that local densities of herbivores can be

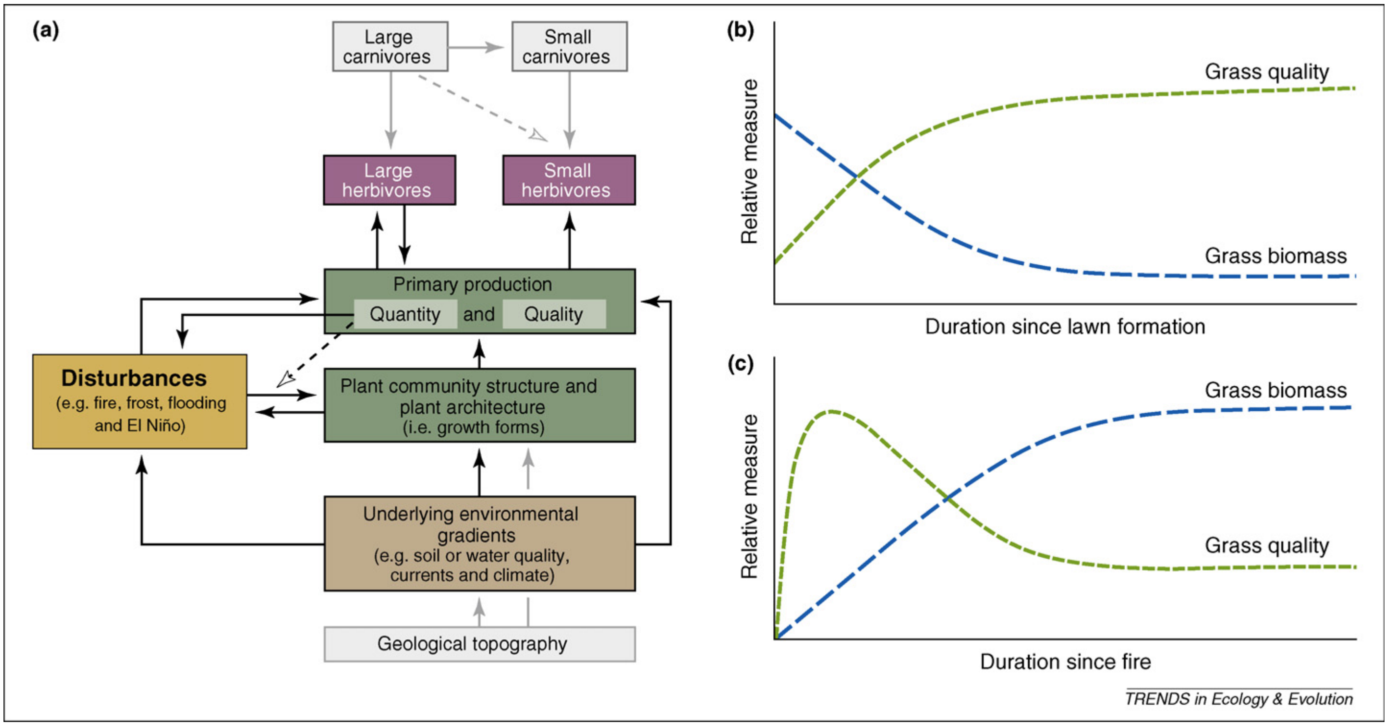

Figure 5. Abiotic and biotic disturbances, such as fires or intense grazing, alter the primary production and the plant community structure of a landscape which, in turn, affects the abundance of different sized herbivores. **(a)** Disturbances can have reciprocal effects (double arrows) on primary production. For example, herbivores can reduce the biomass of grass, which reduces the probability of fire; but, conversely, fires remove grass necromass, which stimulates re-growth of high quality shoots that are preferred by herbivores. Interaction-modifying relationships (dotted arrow) alter the effects of a disturbance, such as large amounts of flammable biomass altering the severity of a fire. Positive feedback loops have additive effects, for example grass biomass increasing the probability of a fire that would remove trees and provide grass with a competitive advantage. **(b)** Biotic disturbances, such as grazing lawns created by white rhino, modify the quality and quantity of vegetation over time by altering the competitive balance between grazing-tolerant and grazing-intolerant grass species [46,50,51]. **(c)** Abiotic disturbances, such as fires, alter the short-term abundance and nutritional quality of the grasses available to herbivores by removing senescent vegetation and stimulating nutrient-rich re-growth [56,61,99]. Long-term species succession could reverse this trend.

regulated by both predation and attributes of the plant community (e.g. structure, quality and quantity), disturbances are factors that can change the primary mechanism of herbivore regulation and lead to nonlinear responses in abundance (Figure 5a) [22,45–47].

Reciprocal effects occur between large herbivores and primary producers (represented with double arrows in Figure 5a) that can lead to grazing facilitation between species [25,48,49]. Mega-herbivores, such as white rhino or hippo, create and maintain low-biomass grass swards composed of nutritious grazing-tolerant grasses, which subsequently support other smaller grazers [50,51]. The repetitive grazing of specific patches by multiple species where more dung and urine are deposited might have similar consequences, resulting in fertile hotspot locations where grazers consistently occur over time [52,53].

Reciprocal interactions alter the probability of a disturbance occurring in an ecosystem, whereas interaction modifiers (as per Ref. [14]) alter the severity of a disturbance. For example, the relative proportion of trees and grasses in a savanna influences its potential flammability [54] because grasses (which senesce seasonally) contribute more to the fuel load than do trees. Once grasses dominate the plant community owing to disturbances such as herbivory (e.g. Ref. [55]), a positive feedback between grass abundance and fire frequency can arise (double arrow in Figure 5a). In addition, the accumulation of grass biomass also alters the intensity of a fire (dotted line in Figure 5a), which when combined with the positive feedbacks between fire frequency and grass abundance, maintains an open grassland landscape, preventing tree invasion [54,56–58]. As a result, fires can prevent invasion of grasslands by trees, which is engineered, in part, by the grazing intensity of herbivores [59,60].

Disturbances such as grazing and fire can act additively in savanna systems by changing the competitive balance between grazing tolerant and intolerant grasses (Figure 5b) [46] and influencing the nutritional quality of the forage supporting herbivores (Figure 5c) [61,62]. Therefore, where some savannas have sufficient rainfall to support closed forests, they persist as mixed grasslands owing primarily to disturbances [46,63]. Thus, two systems with similar rainfall and nutrient regimes could have different woodland–grassland structures because disturbances push systems between multiple states [55,58] and this, in turn, affects the abundance of herbivores.

Emerging properties: top-down and bottom-up processes are not mutually exclusive

The separate roles of predation (Figure 3a), primary production (Figure 4a), or disturbance (Figure 5a) in the regulation of herbivore populations have different consequences when they are combined as opposed to when considered separately. Underlying environmental and landscape gradients affect top-down and bottom-up processes simultaneously [2] by influencing the forage quality and quantity available to herbivores while changing their exposure to predation (Figure 6a). Thus, in Kruger, rainfall

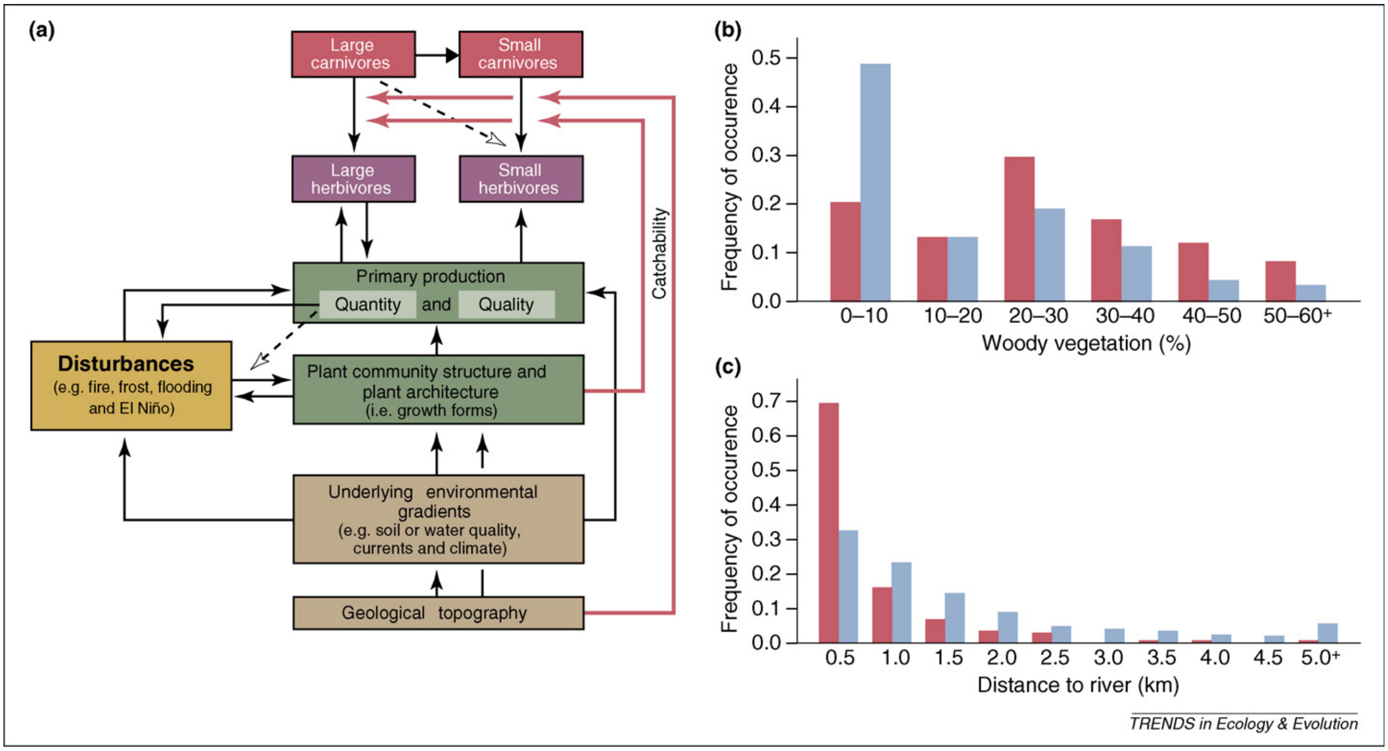

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Figure 6. An ecosystem template of the macroecological processes determining the abundance and distribution of herbivores. **(a)** Underlying environmental gradients simultaneously affect the quality and quantity of forage available to herbivores, and also affect the efficiency of predators at capturing prey. Thus, bottom-up and top-down processes regulating herbivores are not independent. For example, **(b)** lions select areas with denser vegetation (red bars), and **(c)** areas that are closer to rivers for hunting more often than expected (red bars), based on the availability of these resources across the landscape (blue bars). Therefore, the plant community structure (such as percentage tree cover) and topographic features (such as rivers) contribute to the predation risk for herbivores, while simultaneously influencing the quality and quantity of forage available to them. Data from Ref. [66].

simultaneously affects predation and primary production [64]. Moreover, the topography of the landscape (e.g. hills, catenas and rivers) affects the quality and abundance of primary production available to herbivores [7,22,45], while simultaneously determining the amount of cover for a predator, and increasing predators' hunting success by concealing them from their prey (Figure 6b, c) [65–69]. These indirect (Figure 4a), additive (Figure 5a), reciprocal (Figure 5a) and interaction-modifying (Figure 5a) relationships strengthen the interdependencies between primary production, disturbances and predation in regulating herbivores (Figure 6a).

The scale of heterogeneity determines the mode of regulation

Top-down and bottom-up processes are modified by the scale of both spatial and temporal heterogeneity [70]. Suitable habitats can occur heterogeneously at a coarse scale where large patches are separated by long distances, or as a fine-scale mosaic [71,72]. When heterogeneity is coarse, herbivores migrate long distances between suitable patches. When habitats are locally heterogeneous, animals move frequently between small patches but do not move far. On a temporal scale, strong seasonality causes animals to move between patches as phenological conditions change (such as the seasonal drying of grass), whereas weak seasonality enables animals to remain in local areas. The consequences of these different scales are seen in the long-distance seasonal migrations of wildebeest (*Connochaetes taurinus*) in Serengeti, Coke's hartebeest (*Alcelaphus buselaphus*) on the Athi plains of Kenya, or white-eared kob (*Kobus kob leucotis*), topi (*Damaliscus lunatus*) and Mongalla gazelle (*Gazella thomsoni albonotata*) in Sudan [1]. Such movements reduce the impact of predation as predators cannot follow the herbivores over these long distances [73,74] and result in bottom-up regulation [34] (Box 1). By contrast, fine-scale spatial and temporal heterogeneity keeps herbivores within the territories of predators and results in top-down regulation. This distinction is seen by comparing resident wildebeest in Pilanesberg, Hluhluwe-iMfolozi, Kruger (South Africa), Ngorongoro Crater (Tanzania), and Etosha (Namibia) [4,75–78] which are predator regulated, to migrant wildebeest in Serengeti [34] which are food regulated (Box 1). Therefore, abiotic gradients influencing the regulation of herbivores at large scales through predation and nutrition are replicated at finer scales and determine how animals are distributed over a landscape [79].

Abiotic gradients determine the direction of regulation

The availability of abiotic factors, such as soil nutrients and rainfall, determines the mode of population regulation of herbivores [2,80]. High nutrient supply, such as in volcanic or riparian soils, leads to higher quality plant forage, as seen in eastern Kruger, southern Serengeti and Samburu (Kenya) [70,81]. Plants with high nutrient content and low amounts of fiber can support animals of small body size that are top-down regulated. By contrast, sandy soils of granitic origin are low in nutrients, and result in fibrous plants that are less digestible. Such plants

Box 1. Adaptive responses to regulation: migrations, crypsis and vigilance

Large herbivores are occasionally found in areas of low plant biomass whereas small herbivores are sometimes found in areas of high plant biomass, contrary to the expectations of Figure 7 (main text). The realized niche of many herbivores differs from expected because they escape regulation through behavioral and physiological adaptations selected through evolutionary time [26].

For example, migrations enable a population to escape the limitations of both low forage biomass and predation. By sequentially moving between the best available food patches, migrants increase the total available biomass of highest quality food, without exhausting the overall food supply. Small resident populations of wildebeest in Pilanesberg, Kruger and Serengeti are regulated by predation [64,77], whereas the large migratory wildebeest population in the Serengeti (~1.2 million) are regulated by the availability of sufficient forage, especially during the dry season when food is most limited [34]. Other resident herbivore species in Kruger (e.g. roan antelope, *Hippotragus equinus*) and Serengeti become more predator regulated in areas they share with migrant populations, because the seasonal influx of migratory prey supports more predators that tend to supplement their diet with resident prey [80]. As a result, the abundances of migrants versus residents can differ by orders of magnitude [73,74,76]. In circumstances where migratory routes are blocked, the population declines rapidly [1] and becomes predator regulated. Migrations explain how large herbivores can persist in low biomass areas, such as the paradox of mammoths that occupied the low biomass habitats of the tundra. Other behavioral adaptations to predation include group dilution and group vigilance, where individuals decrease their probability of being caught [96].

Avoiding predators through habitat selection or crypsis requires physiological adaptations. For instance, addax (*Addax nasomaculatus*), gemsbok (*Oryx gazelle*) and Arabian oryx avoid predators by living in arid habitats; however, they require complex adaptations for water retention and cooling [97]. Digestive adaptations are required especially by small, energetically constrained herbivores relying on crypsis in thick low-quality vegetation [98]. In both circumstances, populations escape predation but become regulated at much lower densities by forage quantity and quality, respectively.

are eaten by large herbivores, such as elephants and buffalo, which are bottom-up regulated [29,42,82]. This gradation forms the basis for our interpretation of the different savanna systems in Africa, which we describe below.

Synthesis: Shifting regulation across gradients of productivity in African savannas

The integration of allometric differences in susceptibility to top-down and bottom-up regulation along gradients of productivity enables an interpretation of the various herbivore dynamics across African savannas (Figure 7). The relative importance of predation, forage quality and forage abundance in regulating grazers should change under different rainfall and soil fertility regimes. Figure 7 proposes how different areas in Africa, often with functionally similar species, could be regulated by different mechanisms along gradients of rainfall and soil fertility [27–29].

The highest vegetative biomass occurs with high water availability (rainfall or flooding) on fertile soils usually of volcanic or fluvial origin seen best in the Ruwenzori grasslands (Uganda), the Nile floodplains and the flooded Boma grasslands of southwest Sudan (Figures 3b,6a) [61,83–85]. Under these moist, fertile conditions, the quantity of food is effectively unlimited and, therefore, regulates only the largest herbivores (dashed blue line, Figure 7a). However, high rainfall causes the grass to have a large proportion of poor-quality stems, making digestion more difficult and reducing the overall nutritional quality (dashed green line, Figure 7a). The high standing biomass under high rainfall conditions also conceals predators, making small grazers more susceptible to top-down effects (solid red line, Figure 7a). As a result, under high rainfall and fertile conditions, small herbivores become regulated by predation, as in the Ruwenzori system [86], whereas medium and large herbivores are regulated by the quality of the available forage because the quantity is effectively limitless.

By contrast, forage quality is highest under low rainfall conditions on fertile soils, such as on the open treeless Serengeti plains and the saline soils of Etosha. Here, the low grass biomass exposes predators making them visible to herbivores, and results in minimal top-down regulation. Instead, the low quantity of forage regulates the number of medium and large grazers, with predation accounting for most of the mortality in only the smallest size classes (Figure 7b) [41]. The quality of the grass has little impact on regulating populations, because nutritious forage is abundant and readily available.

The nutritional quality of grass is lowest in high rainfall areas with infertile soils and, therefore, becomes more important in regulating herbivore populations (Figure 7c). Such areas can be found in the broad-leaved miombo woodlands of the south and central African plateau, such as Selous (Tanzania), Hwange (Zimbabwe), Chobe (Botswana) and Kafue (Zambia), the coastal sand dune savannas of St. Lucia (South Africa) and the Maputu Elephant Reserve (Mozambique), and the moist savannas of Garamba (DRC) and Mole (Ghana) [29,87–89]. In these communities, there is a high biomass of woody vegetation but also of tall grasses of lower nutritional value, which support fewer herbivores and predators than areas with fertile soils. Predation is expected to be high because the high grass biomass conceals predators, making them more effective [66,68]. The requirements of small herbivores for high quality forage combined with their susceptibility to predation limit their abundance in these areas (Figure 7c). The dominant grazers are elephants [29,89]. Even megaherbivores might not be able to escape the limitations of quality because the methane production associated with ingesting a lot of low quality food reduces their capacity to absorb nutrients [39].

Semi-arid systems with infertile soils, such as Tsavo and Samburu (Kenya), and the Kgalagadi Transfrontier (South Africa and Botswana), tend to have sparse and nutritionally poor plants, supporting lower herbivore densities and, as a result, fewer predators [29,90,91]. These conditions are more extreme in desert environments, such as the stony plains of the Jiddah (Oman) home of the Arabian oryx (*Oryx leucoryx*) [92], and the Ouadi Achim Faunal Reserve (Chad) where the scimitar-horned oryx (*O. dammah*) used to live [93], and the Skeleton Coast (Namibia). Under these conditions, predation does not limit herbivore abundance. Herbivores are regulated by forage quality (especially for smaller herbivores) and forage quantity (for larger animals) (Figure 7d).

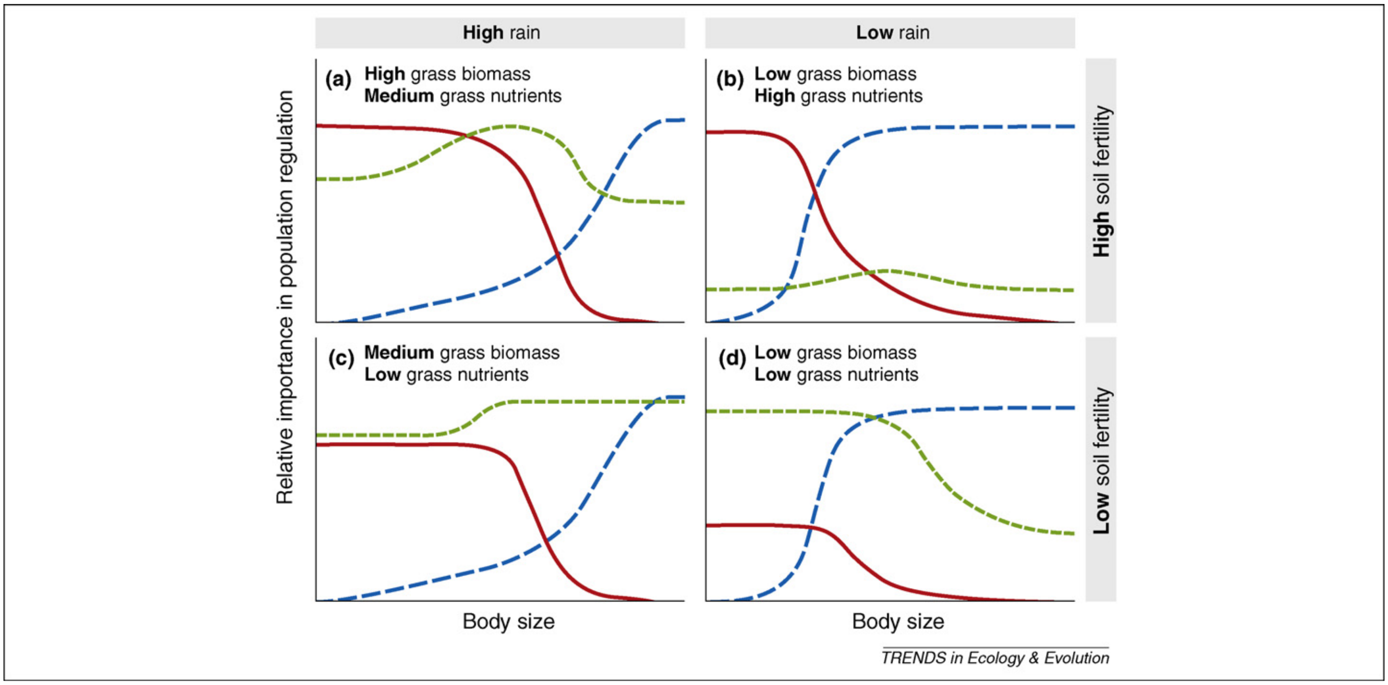

Figure 7. Predictions of the relative importance of predation (solid red line), food quality (dotted green line) and food abundance (dashed blue line) in regulating herbivores of increasing body mass across rainfall and soil fertility gradients, assuming all else is equal (e.g. availability of drinking water, size and isolation of protected area, etc.). We consider herbivores between 10 kg and 1000 kg, with a major portion of grass in their diet [33]. **(a)** High rainfall and soil nutrients. Food abundance regulates large herbivores, food quality regulates medium-sized herbivores and predation regulates small herbivores. **(b)** Low rainfall, high soil nutrients. Food quality does not regulate. Food abundance regulates large and medium-sized herbivores, predation regulates small ones. **(c)** High rainfall, low soil nutrients. Food quality regulates all herbivores, with predation acting synergistically at small size, and food abundance at large size. **(d)** Low rainfall and soil nutrients. Predation is not regulating, food quality acts at small size and food abundance at medium and large sizes. For more details see main text. If rainfall patterns change owing to global warming, herbivore regulation within a savanna ecosystem is predicted to shift from (a) to (b), or (c) to (d), or *vice versa*.

Conclusions and future directions

Predation and competition for resources interact synergistically rather than operate independently [94]. Reciprocal, indirect, additive and interaction-modifying relationships shape this synergism to explain functional differences between ecosystems. In essence, the interplay between: (i) the availability of limited abiotic resources (such as nutrients and rainfall) that determine the quality and quantity of primary production; (ii) the evolutionary trade-offs related to body size (including predation sensitivity, digestive capacity and metabolic requirements); (iii) adaptive behaviors (such as migration or group vigilance), which enable primary consumers to escape regulation; and (iv) the extent and frequency of disturbances (such as fires, storms, extreme temperatures, salinity shifts, scouring, etc.) are processes affecting how predation and competition collectively structure communities. This conceptual structure yields testable predictions for how global environmental changes might affect the distribution of different sized herbivores and potential regime shifts in ecosystem dynamics [95]. For example, changes in rainfall owing to global warming could shift the importance of food and predation in regulating herbivore populations, so that decreasing rainfall would push an ecosystem along the x-axis in Figure 7 from (a) to (b), or (c) to (d). The evolutionary role of early hunter-gatherer humans in regulating herbivores as predators and as agents of disturbance fits the framework of Figure 6. However, modern humans have escaped from factors regulating their population density, which destabilizes this framework.

Future research should test the predictions of Figure 7. However, in order for this to occur, more data are required to resolve the consequences of predation. Specifically, the analysis of herbivore carcasses suggests small prey are prone to many predators (i.e. size-nested predation, Figure 2a) [3], but this is not supported by data on carnivore diets, which suggest that predation is size partitioned (Figure 2b) [4]. In addition, an evaluation of mortality in juvenile age classes might show that predation by a single predator, with low capture rates, could still impose strong population regulation, especially for larger species.

In summary, we propose that abiotic factors determine the importance of predation, forage quality and forage abundance in regulating herbivores of different sizes (Figure 7) and this alters the relative strength of the connections between biotic and abiotic components in ecosystems (Figure 6a). The availability of key environmental resources has profound consequences for herbivore regulation and ecosystem dynamics by simultaneously affecting multiple top-down and bottom-up processes. The different herbivore dynamics of the many savanna systems of Africa can be understood in the context of this framework. These concepts could help our understanding of other ecosystems where strong abiotic gradients influence the shape of the community (such as salinity and desiccation in intertidal ecosystems, dissolved oxygen and opacity in aquatic ecosystems, or body mass and predation risk in avian communities). The strength of this framework is that it captures how environmental gradients can switch top-down and bottom-up processes that regulate animal abundance.

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