Review Article

Top-down and bottom-up control of large herbivore populations: a review of natural and human-induced influences

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Abstract
The question whether animal populations are top-down and/or bottom-up controlled has motivated a thriving body of research over the past five decades. In this review I address two questions: 1) how do top-down and bottom-up controls influence large herbivore populations? 2) How do human activities and control systems influence the top-down and bottom-up processes that affect large herbivore population dynamics? Previous studies suggest that the relative influence of top-down *vs*. bottom-up control varies among ecosystems at the global level, with abrupt shifts in control possible in arid and semi-arid regions during years with large differences in rainfall. Humans as super-predators exert top-down control on large wild herbivore abundances through hunting. However, through fires and livestock grazing, humans also exert bottom-up controls on large wild herbivore abundances through altering resource availability, which influences secondary productivity. This review suggests a need for further research, especially on the human-induced top-down and bottom-up control of animal populations in different terrestrial ecosystems.

Keywords: Ecosystem, predation, primary production, savanna, trophic level

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Introduction

Top-down and bottom-up processes are thought to play important roles in the control of large herbivore populations in terrestrial ecosystems [1-4]. However, the strength and role of such processes may vary spatially and temporally [5, 6]. Moreover, human activities can potentially affect both top-down and bottom-up processes in terrestrial ecosystems. Humans are a keystone species that alters terrestrial ecosystem structure and composition through actions such as setting fires and livestock grazing (human-induced bottom-up control), and by acting as a generalist super predator able to top-down harvest any animal species regardless of body mass [7, 8].

Moreover, globally, ecosystems are under pressure as a result of human population increase and climate change [7, 9]. For instance, biodiversity in tropical countries is under increasing threat from illegal resource use, poaching, habitat fragmentation, encroachment into wildlife areas, high variability in weather patterns and disease occurrences, which all alter the natural control processes of large herbivore populations [10-12]. Such threats have led to increasing debates on the appropriate approach for the conservation of both evolutionary processes and the ecological viability of populations [13, 14]. For example, some recent approaches emphasize large-scale conservation of mosaic landscapes with different habitats, exemplified by ecosystem-based management policies for transboundary conservation areas or transfrontier conservation areas in southern Africa [15]. However, some conservationists argue that conservation efforts should target the fine scale such as genes, populations and species [13].

Human activities are, however, influenced by policy instruments, incentives and other control systems to mitigate impacts of human activities on large herbivore populations [16]. For example, in most tropical countries integrated development and conservation projects (ICDPs), including community-based natural resources management programmes, have been implemented in areas bordering protected areas to promote poverty alleviation, rural development and wildlife conservation through sustainable use of natural resources [17, 18]. However, the effectiveness of ICDPs in meeting the desired objectives still needs evaluation given the diversity of conservation projects throughout tropical countries [e.g., 19].

Improving our knowledge about the role of natural and human-induced top-down and bottom-up controls of large herbivore populations in terrestrial ecosystems is, therefore, vital in advancing scientific knowledge and in the long-term management and conservation of ecosystems. In this review I focus on terrestrial ecosystems and address two questions: 1) how do top-down and bottom-up controls influence large herbivore populations? 2) How do human activities and control systems influence the top-down and bottom-up processes that affect large herbivore population dynamics?

Population control in ecosystems

The relative importance of top-down and bottom-up processes in the control of both aquatic and terrestrial organisms has been a subject of research and considerable debate among ecologists [3, 20-22]. In 1960, Hairston et al. proposed a simple conceptual model for the dynamics of terrestrial communities. They suggested that communities consisted of four groups of organisms (carnivores, herbivores, plants and detritivores), and that their trophic interactions explained why green plants dominate the earth and also why organic biomass does not accumulate. Briefly, Hairston et al. [20] argued that plants dominate natural communities because carnivores control herbivore abundance, thereby freeing vegetation from herbivore control. Hairston et al. [20] also suggested that detritivores were resource-limited, thus preventing accumulation of organic matter on a global basis. This simple framework suggested that carnivores and detritivores were limited by competition and that herbivores were controlled by direct predation, and that carnivores indirectly influenced plant abundance. The overall perspective was that ecological communities are controlled by processes whose effect flowed down the food chain; this was later termed top-down control [5].

The alternative view of bottom-up control was the implicit partner of succession theory as developed by plant ecologists [23]. This perspective held that since plant primary production fueled the animal biota, plants, along with nutrients and light, controlled animal communities from the bottom of the food chain upward to higher trophic levels [24]. This perspective was, however, not widely accepted by ecologists, perhaps because, in part, plant and animal ecologists interpreted the term 'control' differently, but also because examples could be cited that supported either perspective [25]. Moreover, in the 1960s, populations of some species of large carnivores declined due to dichlorodiphenyltrichloroethane (DDT) use [26], hence, predators role in top-down control of large herbivore populations was viewed as minimal. However, in the 1980s and especially 1990s the populations of several predator species increased following the ban of DDT use in the late 1980s [27].

The current understanding is that both top-down and bottom-up processes influence the size of wild herbivore populations [2, 28]. Their respective strengths vary between different ecosystems, and their relative importance can vary spatially and temporally, with possible abrupt shifts in top-down and bottom-up control occurring over time [6, 28]. Abrupt shifts in top-down and bottom-up control may occur in arid and semi-arid ecosystems with strong inter-annual variation in rainfall [29]. In prevailing dry years, resource-limited conditions lead to strong bottom-up control because of reduced plant productivity, and perhaps reduced seed and insect resources. During wet years, biotic interactions become more important as the abundance of consumers increase and the forces they exert on lower trophic tiers become more prominent; consumers have a greater effect on their resources, and top-down control prevails [6].

Top-down population control of large herbivores in terrestrial ecosystems

Predation plays a key role in controlling populations of large herbivores (>5 kg body weight) in tropical ecosystems, especially the non-migratory species, illuminating one of the features defining the landscape of fear that large ungulates exist within [30, 31]. Top predators may structure a whole community by initiating a trophic cascade [32]. A trophic cascade occurs when a consumer influences at least two other trophic levels, such as when a predator limits the populations of its prey, which in turn limits the populations of its own prey [31]. For example, several North American studies have reported cascades where top carnivores, such as wolf (*Canis lupus*), cougar (*Puma concolor*) or grizzly bear (*Ursus arctos*), affect ungulate density and foraging patterns, with indirect, positive effects on plant species or communities [22, 33, 34]. Recent evidence, however, suggests that: i) there is little consensus on the occurrence of trophic cascades in terrestrial ecosystems, ii) trophic cascades are quite variable, and iii) trophic cascades are influenced by ecological complexity of the community and anthropogenic influences, thus challenging past findings on the role of large carnivores in ecosystems [35].

The widespread extinctions of top predators as a result of hunting (pursuing a living thing for food, for sport or for trade), persecution by humans, and habitat loss have changed terrestrial ecosystem structures through mesopredator release associated with trophic cascades, where increased abundances of medium-sized predators may have detrimental effects on prey communities [36, 37]. For example, populations of red fox (*Vulpes vulpes*), a mesopredator, have increased following the decline of top predators such as wolves and Eurasian lynx (*Lynx lynx*) due to agricultural expansion in Sweden [38]. The mesocarnivores, small to midsized species (<15 kg) are generally more numerous and diverse than larger carnivores and often reside in closer proximity to humans [39].

Among the African savanna herbivores, Sinclair et al. [30] have argued that populations of smaller-bodied species are controlled by predation, whereas populations of larger-bodied species (≥150 kg) are limited by forage availability. The relative body size strongly determines: a) relative kill success for particular size classes of prey species and b) dietary dependency on different body size ranges of prey

[4, 40]. Only above a body mass of around 1,000 kg do mammalian herbivores become generally free of predation, except on immature animals, and hence are almost solely food-limited [4, 40].

Bottom-up population control of large herbivores in terrestrial ecosystems

All trophic levels are potentially limited by availability of food resources [24]. Contrary to top-down control, Slobodkin [41] argued for a bottom-up control that follows the classical laws of thermodynamics, i.e., energy is transferred and converted to potential energy through radiant energy to green plants and finally to a chain of organisms. Therefore, biomass production at all trophic levels is ultimately dependent on the quantity and quality of resources comprising the basal trophic level [42]. Thus, changes at the bottom of the food web can have an effect on the entire food web. In most natural communities, densities of large herbivores drop sharply during inclement seasons, e.g., temperate winters, or following major disturbance such as flood, fire, landslide or drought [43]. High rainfall variability is an important factor influencing the population dynamics of large herbivores, operating directly on individuals and through its effect on forage characteristics [44]. Preisser [42] suggests that the bottom-up effects of increased productivity at the basal trophic level may influence the strength of top-down control in a system and the patterns of biomass accumulation at subsequent trophic levels.

Population control in species-poor and species-rich terrestrial ecosystems

The relative importance and strength of top-down and bottom-up controls on mammal populations differ between species-poor and species-rich terrestrial ecosystems. Species-poor ecosystems are largely characterized by low secondary productivity [45], and predator-prey systems with only one major predator and a few prey species, such as in temperate woodlands and tundra [46]. In these ecosystems, it is suggested that bottom-up control of prey is dominant, with a few exceptions of top-down control of prey [28]. Although population control of prey by their predators, for instance, in North America and Canada, may result in regular periodic fluctuation in population size (cycles), bottom-up processes are still key to those fluctuations [47]. However, recent evidence suggests less strong small herbivore cycles associated with a reduction in winter population growth across Europe, although the role of bottom-up processes responsible for cyclicity have not been lost [48].

Species-rich ecosystems, or high diversity systems of large mammal herbivores and carnivores, are mostly associated with tropical savannas [49]. In species-rich ecosystems, large predators exploit a wider range of prey sizes, very large herbivores being less affected by predation [50, 51] and smaller ungulates having many more predators than larger ungulates. Thus, smaller ungulates experience more predation and are potentially predator controlled whereas large herbivores (≥150 kg) are mostly bottom-up controlled [4, 28, 52].

The human factor on top-down and bottom-up control in animal communities

a). Top-down control: human influence

Recent studies suggest that humans precipitated the extinction of large carnivores and herbivores in many parts of the globe through combined direct (hunting) and perhaps indirect impacts, for example, competition, habitat alteration and fragmentation [53, 54]. On continents worldwide, about 90 genera of mammals weighing ≥44 kg have disappeared [55]. Under the overkill hypothesis, extinction occurs because hunting causes death rates to exceed birth rates in prey species [56]. It has been suggested that anthropogenic factors such as selective hunting of large mammals by recently arrived humans played an important role in the extinction of the megafauna in North America, South America and perhaps other landmasses, compared to the minor role that changes in climate and vegetation played at the end of the Pleistocene [53, 56, 57]. Similarly, Charles Kay developed an "aboriginal overkill" hypothesis, which asserts that prehistoric wildlife numbers were low, a consequence of hunting by Native Americans who numbered 100 million or more in pre-Columbian North America, resulting in the suppression of wildlife numbers and allowing wildlife browse to proliferate [58]. However, other authors have criticized Kay's "aboriginal overkill" hypothesis, largely based on lack of convincing data [e.g., 59].

Human hunting, therefore, merely adds to the cumulative number of deaths by some critical amount, and the extinction could be sudden or gradual. Hunting in most countries is subject to rules and regulations that hunters must abide by, and any violations are punishable by law [e.g., 60]. The extent of human hunting impacts on large herbivore populations in terrestrial ecosystems varies with rainfall, secondary productivity, abundance and diversity of large herbivores in biomes [Fig. 1, 61, 62, 63]. Species that have slow life histories [64], for example, most large bodied herbivores, would be more susceptible to extinction under any environmental or anthropogenic impact that target slow breeders [55]. For example, in much of tropical forest ecosystems in Africa and Latin America, populations of many large-bodied wildlife species have already declined or were extirpated because of habitat loss and hunting, leaving a fauna predominantly characterized by fast life histories, i.e., small-bodied and rapidly reproducing species [65-68].

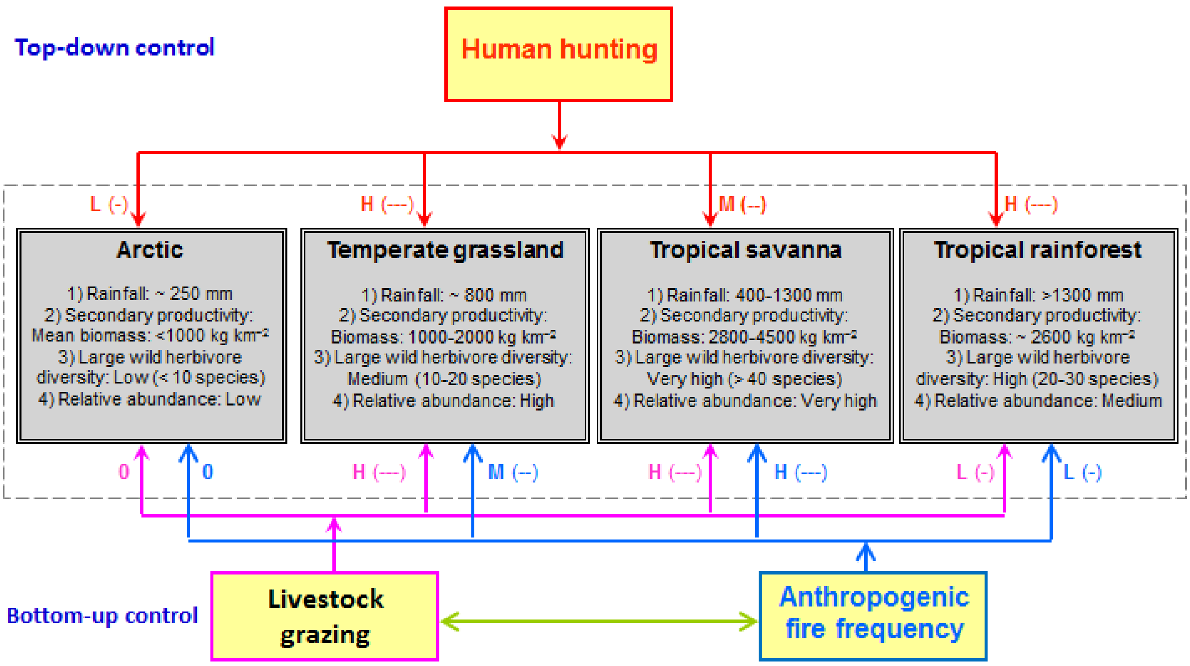

Fig. 1. A schematic representation indicating the top-down and bottom-up controls of human activities (at global biome level) particularly on wild large herbivore community in the arctic, temperate grasslands, tropical savannas and tropical rainforests. Data sources: Barnes and Lahm [61], Du Toit and Cumming [62], Sala et al. [63]. Notes: H = high negative impact, M = medium negative impact, and L = low negative impact. *Impact* refers to negative human influence on specifically wild large herbivore populations and composition occurring in the various biomes, if and only if the outlined respective biome characteristics are satisfied.

Across much of the globe, humans have reduced the range of large carnivores through widespread poisoning, trapping and hunting [69, 70]. In addition, the loss of top predators due to human persecution alters trophic cascades, which may lead to habitat degradation, species loss and even ecosystem collapse [8, 71, 72]. Human-introduced diseases have also altered the natural top-down controls through death of some large carnivores. For example, following the introduction of canine parvovirus in Isle Royale, United States of America, wolf populations declined, resulting in a switch from top-down to bottom-up control of the moose (*Alces alces*) population [73]. Similarly, the lion (*Panthera leo*) population in Ngorongoro Crater, Tanzania, has become unusually vulnerable to infectious disease in recent years owing to its close proximity to a growing human population, thus, altering the strength of the top-down control in the ecosystem [74].

b). Bottom-up control: human influence

i) Vegetation fires

Besides biotic interactions, external factors such as fire are also considered to be important determinants in shaping large herbivore assemblages. Vegetation fires are a common and predictable feature of the world's grasslands, savannas, Mediterranean shrublands and boreal forests [75, 76]. The extent of fires and their impacts in an ecosystem is largely determined by rainfall and its interaction with herbivory and human activities (Fig. 1). Despite the important ecosystem role played by fire, human activities have altered natural fire regimes relative to their historic range of variability, affecting both the primary production of ecosystems and the strength of bottom-up controls of large herbivores. Moreover, fire may cause nitrogen loss and affects net primary productivity in ecosystems, particularly in the savannas [77].

Recent studies suggest that fires do exert a bottom-up control on large mammal communities. For example, Klop and van Goethem [78] suggest that the response of herbivore communities to fire is likely to be the compound effect of various factors, including changes in habitat structure, resource selection patterns, predator avoidance and biotic interactions such as competition. In addition, the effects of fire on ungulate community structure may depend on the time of burning in the season, the extent of burning and the availability of other high-quality grass swards on, for example, grazing lawns and floodplains. Thus, during the dry season and on a local scale, savanna fires are a major factor governing ungulate community structure [78]. Further, Klop and Prins [79] concluded that species richness and assemblage composition of grazers in African savannas are largely governed by anthropogenic fires that modify the quality and structure of the grass sward.

ii) Livestock rearing

With domestication of animals, agriculture brought about a major shift in the interactions between humans and their surroundings (Fig. 1). Herds of domestic animals, often composed of single species, have replaced more diverse indigenous herbivore communities over very large areas [80]. Previous studies suggest that livestock grazing may cause a significant reduction in the standing crop of forage, and that high diet overlap between livestock and wild herbivores, together with density-dependent forage limitation, may result in resource competition and decline in wild herbivore populations, especially in Africa and Asia [81-83].

Natural resources management systems

The increasing pressure on native animal populations from expanding human and livestock populations and settlements, have resulted in native large herbivore species and their habitats being conserved within a few types of land property regimes: state (or public), private, and communal [84]. The conservation and management of native large herbivore species and their habitats also occur in various mixed types and models in different areas, largely determined by varying institutional types and systems, as well as different forms of governance models. Protected areas are places where major threats can somehow be managed and are the most important tool for biodiversity conservation throughout the world, as well as providing economic and cultural benefits [85]. Protected areas include national parks and biological reserves, and mostly encompass diverse animal species [86]. Private wildlife management areas include game farms and conservancies [87].

Community-based natural resources conservation initiatives have been implemented in some wildlife areas in order to reduce unsustainable exploitation of wildlife and human-wildlife conflicts, whilst also providing local communities with conservation benefits or incentives [88]. For instance, the Communal Areas Management Programme for Indigenous Resources (CAMPFIRE) is a government initiative designed to stimulate long-term development, management and sustainable use of natural resources in Zimbabwe's communal farming areas adjacent to state protected areas [89]. Under CAMPFIRE, local communities realize financial benefits from the management of local natural resources, including wildlife [90]. However, presently there is little evidence that community-based conservation programmes have reduced or even stabilized the amount of illegal activity or human-wildlife conflicts, primarily because these programmes fail to offer sufficient incentives for local communities to stop utilizing wildlife illegally, and also fail to reduce costs from conflicts with wildlife [17, 91]. The effectiveness of the CAMPFIRE programmes remains largely unknown due to the differences in human communities and the recent policy changes in Zimbabwe following the land reforms that occurred since 2000.

Control systems on human activities in natural resources management

Man’s interactions with nature are based on a mix of slowly developed social norms and expectations, and increasingly on more rapidly developed short-term incentives and controls [92]. Control is a deeply entrenched aspect of contemporary human societies, i.e., human behavior is controlled through laws, incentives, threats, contracts, and agreements [92]. Control systems are defined here as the formal and informal rules, regulations, laws, social values and belief systems (or dominant beliefs) that orient and influence human behavior in general (including hunting, grazing, using fire, among others). In wildlife areas, policy instruments are designed to change human behavior in order to minimize its impacts on natural resources. Rowcliffe et al. [93] suggest that since hunters will not comply voluntarily, the protection of vulnerable species can only take place through effective enforcement, for example, by wildlife authorities restricting access to protected areas, or by traditional authorities restricting the sale of protected species in local markets. This suggests that law enforcement is crucial in curbing unsustainable and illegal exploitation of animal populations [60, 94].

Leeuwis and van den Ban [16] outline an instrumental model of policy intervention characterized by two important and interrelated features which can be important in understanding human behavior changes. The first feature is that policy intervention take place after the goals and corresponding policies have been defined, in order to persuade as many people as possible to accept a given policy. The second feature is that communication is used deliberately as a policy instrument (in conjunction with other instruments) in order to steer and direct human behavior, which is thought to be largely predictable [16, also refer to the ‘sorting scheme’ in Fig. 2]. From Fig. 2, a distinction is made between ‘non-voluntary’ (or ‘compulsory’) and ‘voluntary’ behavior.

Compulsory behavior arises from coercion (top-down enforcement) that derives from laws and regulations or constraints caused by restrictive provisions (e.g., a game fence) [16]. For example, hunters may be restricted by punishments, from fines and prison terms to social sanctioning, depending on the enforcement system [95]. On the other hand, voluntary behavior can either be internally or externally motivated [16]. Externally motivated voluntary behavior originates from material and social circumstances or financial impulses (e.g., group pressure, provisions and financial (dis)incentives, including income generation from tourism ventures and selling of local products to visitors) brought by the corresponding policy instruments. Internally motivated voluntary behavior may arise from reasoned opinions (e.g., a conviction that hunting or setting unprescribed veld fires is not proper) that can be influenced by communicative intervention [16], for example, through awareness or educational programmes [96].

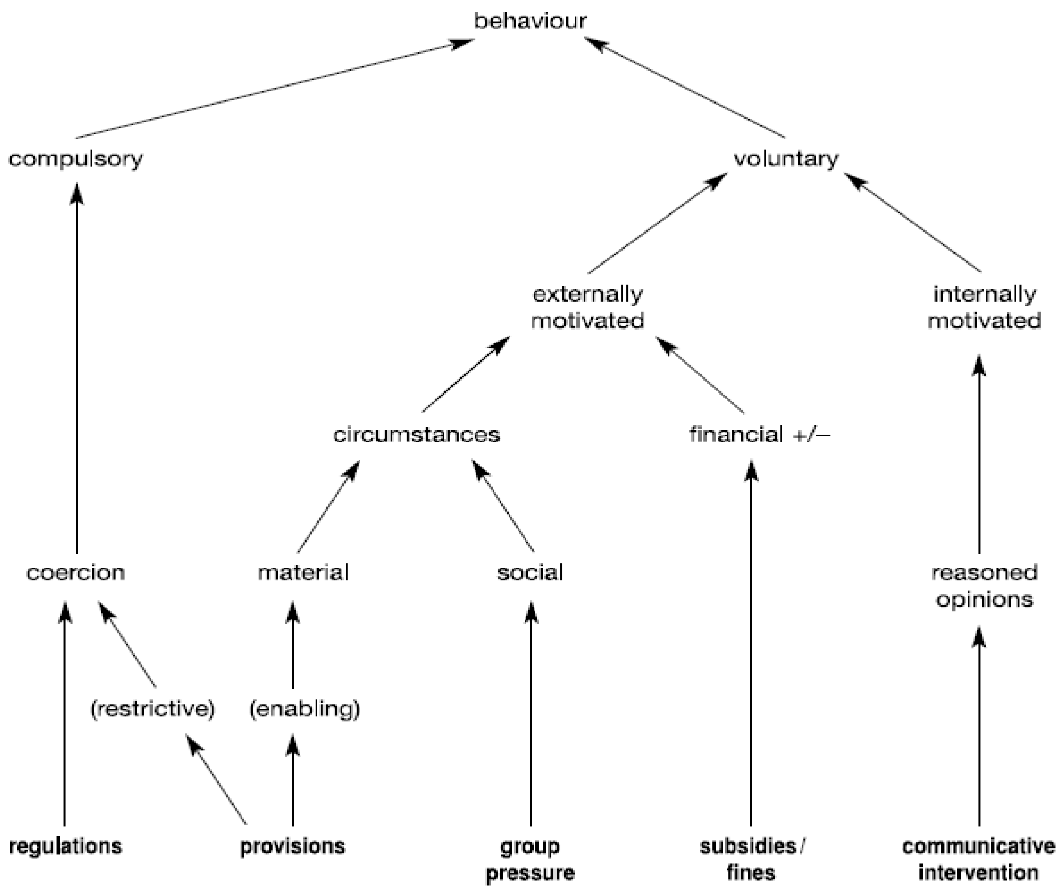

Fig. 2. The relationship between communicative intervention and other policy instruments aimed at stimulating human behavioral change, for example, human activities that affect large herbivore populations. Policy instruments are indicated in bold. Source: Leeuwis and van den Ban [16].

Implications for conservation

Primary productivity is largely influenced by rainfall and soil fertility, with primary production regulating large herbivore population through the classic bottom-up process of resource limitation [see 4]. However, the quantity of primary production is negatively influenced by herbivory and fire. Moreover, human activities can potentially affect both the top-down and bottom-up processes in natural ecosystems.

I suggest some predictions for future research to test, associated with Figure 1. First, related to human-induced top-down control; human hunting is predicted to have a: i) high negative impact on large herbivore populations in tropical rainforests and temperate grasslands, ii) medium negative impact on large herbivore populations in tropical savannas, and iii) low negative impact in arctic ecosystems. Second; anthropogenic fires are predicted to have a: i) high negative impact on primary production in tropical savannas, ii) medium negative impact on primary production in temperate grasslands, and iii) low negative impact on primary production in tropical rainforest and arctic ecosystems. Third; livestock grazing is predicted to have a: i) high negative impact on primary production in tropical savannas and temperate grasslands, and ii) low negative impact on primary production in tropical rainforests and arctic ecosystems.

In conclusion, human impacts are likely to be more severe in tropical areas with high human population densities and high poverty, where human settlements are close to protected areas, and in areas with societal unrest, such as wars and political unrest [10, 60]. Thus, an understanding of institutional policy instruments may also provide a means of mitigating the negative impacts of human activities in and around wildlife conservation areas.

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