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DANGEROUS GIANTS? – LARGE HERBIVORES, FOREST FEEDBACKS AND CLIMATE TIPPING POINTS

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Abstract. Could large herbivores (“megaherbivores”) modify tree-cover sufficiently to disrupt the hydrological cycle? The implications of such interactions are profound: potentially switching climates from wet to arid. Was such instability important in the past? Here, inspired by the suggestions of Gorshkov and Makarieva [1], I review the influence of megaherbivores on forests and examine what we can learn from the largest modern example, the Bush elephant (*Loxodonta africana* Blumenbach). These animals can certainly reduce tree and forest cover, but some tree species appear able to repel, resist or even tolerate them. Furthermore, elephant populations are vulnerable to dehydration, starvation, disease, and predation, and are thus not immune to environmental change and feedbacks. I look at the dynamics of tropical tree cover, and the balance with tropical savannas. I find evidence that megaherbivores can influence tree cover over extensive regions and might, in suitable circumstances, help tip the climate from wet to dry if such a tipping point was close. But the overall story remains complex and human influences obscure our view of key processes. While there are good reasons to believe that megaherbivores could be influential, we neither know nor fully understand the processes that led to past expansion and maintenance of savanna and other fire-maintained biomes. The role of fire and flammable biomes, and the factors – including animals – that may influence them, require more attention. Fire has an appetite considerably larger than that of any megaherbivore.

Key words: disturbance-ecology, elephants, fire, forest-dynamics, *Loxodonta*, megafauna, savanna, tipping points.

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ОПАСНЫЕ ГИГАНТЫ? – КРУПНЫЕ РАСТИТЕЛЬНОЯДНЫЕ ЖИВОТНЫЕ, РЕАКЦИЯ ЛЕСА И КРИТИЧЕСКИЕ КЛИМАТИЧЕСКИЕ СОСТОЯНИЯ

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Аннотация. Могли бы крупные растительноядные животные (“megaherbivores”) модифицировать древесный покров до такой степени, чтобы разрушить круговорот воды? Последствия таких действий значительны, вплоть до изменения климата от влажного к засушливому. Играла ли эта неустойчивость существенную роль в прошлом? В этой статье, принимая во внимание предположения работы Горшкова и Макарьевой [1], приводится обзор воздействия крупнейших растительноядных животных на лес с более подробным рассмотрением на примере наиболее крупного из существующих растительноядных – саванного слона (*Loxodonta africana* Blumenbach). Эти животные, несомненно, могут существенно уменьшать древесный и лесной покров, но некоторые виды деревьев, как представляется, способны противостоять слонам, выдерживать их воздействие или даже сосуществовать с ними. Более того, сами слоны подвержены воздействию хищников, обезвоживанию, голоду и болезням, а потому не защищены от изменений окружающей среды. Рассматривается динамика тропического лесного покрова и его баланс с тропическими саваннами. Представлены данные о том, что крупнейшие растительноядные животные действительно могут свести лесной покров на нет на значительных площадях и могли в соответствующих условиях подтолкнуть климат к переходу из влажного в сухое состояние, если такая критическая точка была достаточно близка. Но в целом проблема остаётся

сложной, и воздействие человека препятствует ясному пониманию ключевых процессов. Хотя есть достаточные основания считать, что крупнейшие растительноядные могли оказывать на экосистемы большое влияние, мы не знаем и полностью не понимаем те процессы, которые в прошлом привели к распространению и поддержанию саванны и других биомов, зависящих от пожаров. Роль пожаров и подверженных горению биомов, а также факторов (включая и животных), которые на них влияют, заслуживает большего внимания. “Аппетит” у пожара существенно превосходит таковой у любого из крупнейших растительноядных животных.

Ключевые слова: экология возмущений, слоны, пожар, лесная динамика, *Loxodonta*, мегафауна, саванна, критические точки.

Благодарности. Для меня большая честь выступить с этим комментарием, и я надеюсь, что я воздал должное этим идеям. Если бы мы только могли обсудить их с Виктором Горшковым, я уверен, что мы продвинулись бы дальше. Его творческих идей, анализа и юмора будет не хватать. Я благодарю Анастасию Макарьеву за приглашение к этому комментарию и Алексея Алейникова за редакционные рекомендации. Бадре Мугерва любезно предоставил изображения для первого рисунка. Я также благодарю Анастасию Макарьеву, Штайн Мо, Ричарда Бишофа, Мириам ван Хейст, Райана Бёрнера, Йенни Катарину Бредин, Джозефа Хауза, Ларису Ханину и анонимного рецензента за полезные отзывы, включая важные пояснения и предложения, к более ранним версиям статьи.

Preamble

Gorshkov and Makarieva [1] weave together multiple themes – including energy flows, metabolic processes, geometric limits and powerful climatic feedbacks – to suggest that large animals can reach densities that remove sufficient tree cover to “claim all ecosystem productivity” and undermine climatic stability. To investigate these suggestions, I examine large herbivores (“megaherbivores”) and the stability of forests and other tree cover. Though crucial, I shall not explore the influence of tree cover on rainfall as this is a subject I have discussed and summarised in detail elsewhere [2]. In brief, the proposal is that large-scale tree cover sustains rainfall within continents through powerful positive feedbacks and loss of tree cover reduces these feedbacks and can result in a catastrophic switch of states where well-watered regions become arid. My focus here is on what we know or might infer about the impacts of large animals on tree cover with a focus on examples I am familiar with: Bush elephants and tropical vegetation. While, as a field ecologist, I often take a detail-oriented approach, I appreciate how elegant theoretical reasoning encourages us to look further and deeper.

I have organised this commentary by sections summarising evidence, theory and unknowns around selected themes pertinent to the larger puzzle. *The Giants* overviews megaherbivores both past and present. *Elephants and Tree Mortality* summarises the direct impacts of elephants on trees and tree cover. *Population Growth and Constraints* asks what factors can, or might, govern elephant populations. *Savannas in an Evolutionary Context* explores how modern savannas arose and how both fire and herbivory influenced the evolution of these biomes. *Savanna-Forest Dynamics* looks more closely at the processes governing savannas and tree cover with an emphasis on fire. *Animal Influences* notes the complexity of understanding outcomes that depend upon multiple processes, including animals. *Conservation Comments* clarifies the interpretation of the ecological role of mega-

herbivores. In the final section, *Synthesis*, I combine the puzzle pieces to reveal the overall picture.

The giants

Our world has lost many giants. There is considerable uncertainty on size estimates [3] but the largest ever terrestrial animals were likely the long-necked dinosaurs such as South America’s ~73 tonne *Argentinosaurus huinlensis* (Bonaparte & Coria¹) and Africa’s ~60 tonne *Paralititan stromeri* (Smith *et al.*) [4]. Such sizes may have been an adaptation to feeding on trees, with an apparent correlation between the occurrence of long-necked sauropods and forest [5, 6]. The largest terrestrial mammals were likely the extinct ~16 tonne Eurasian mammoth *Zygodolophodon borsoni* (Hays) [7] or the extinct hornless rhinoceros *Indricotherium transouralicum* (Pavlova), that achieved 11 to 17 tonnes [7, 8].

Of the 42 terrestrial mammals surpassing one tonne that existed 20,000 years ago just eight remain [9, 10]. Several more giants, including Europe’s hippopotamus species, e.g., *Hippopotamus antiquus* Desmarest, *H. major* Cuvier and *H. gorgops* Dietrich, were lost prior to this period too. The loss of such animals – many of which are judged to have been “ecosystem engineers” having a major impact on the biomes in which they occurred – has many potential implications for vegetation structure and composition in the biomes from which they departed [11, 12] (implications which I discuss in subsequent sections). We remain unsure about the typical sizes, behaviours, and distributions of many of these species as remains are sparse and often enigmatic. Isotopic data can estimate the fraction of C4 vegetation (mainly grasses) in paleo-diets [e.g., 13, 14]. Tooth morphology and wear can indicate other aspects of diet [e.g., 15], but we cannot be certain how animals impacted vegetation.

¹ I provide the accepted taxonomic name and authority (in brackets) at first mention.

A few thousand years ago, animals in the order Proboscidea (“the proboscideans”) occurred across all the continents except Australia and Antarctica. Eurasia’s woolly mammoth (*Mammuthus primigenius* Blumenbach) achieved seven or eight tonnes and became extinct only around four thousand years ago [16], while North America’s *M. columbi* (Falconer) spp. surpassed ten tonnes [7], the Asian *Stegodon zdanskyi* (Hopwood) exceeded twelve tonnes and some of South America’s Gomphotheriidae (e.g., *Cuvieronius* spp.) exceeded four [4]. All these likely included some browse in their diets [e.g., 14, 17]. The Elephantidae, the only surviving family of the order, arose in Africa within the last ten million years. These included not only the extinct mammoths but also Europe’s straight tusked elephants *Palaeoloxodon antiquus* (Falconer & Cautley) that reached 15 tonnes, and were extinct thirty-thousand years ago [18]. Genetic data show that the latter were most closely related to Africa’s extant (and smaller) Forest elephants (*Loxodonta cyclotis* Matschie)² [19]. Investigations suggest all these animals grazed and browsed, including coarse woody materials in their diets [20].

Proboscideans are not the only giants we lost. For example, the Woolly rhinoceros (*Coelodonta antiquitatis* Bronn) reached two tonnes or more and was common throughout Europe and northern Asia before going extinct around 10,000 years ago [21]. Isotopic analysis of horn proteins suggests a seasonal diet with summer grazing and winter browsing [22]. Other European megafauna included several hippopotamuses, and the cave bears (*Ursus spelaeus* Rosenmüller), which occasionally reached one tonne in size – though likely opportunistic omnivores, these bears appear to have been primarily herbivorous [23, 24]. In the neotropics the ground sloths included several large species, such as *Megatherium americanum* (Cuvier) that reached four tonnes [25] and browsed [15, 26]. In Australia, the wombat-like *Diprotodon optatum* (Owen), a part-time browser, reached over two and a half tonnes [27, 28]. The list could continue.

Modern day ecology is an imperfect guide to the past: people and domestic animals have impacted much of the planet. The biomass of domestic animals now exceeds that of modern wild mammals and likely surpasses what was present in the Pleistocene [29]. Aside from the forest cleared for ranching, the replacement of native wildlife with livestock has likely had many more subtle impacts. For example, it has likely contributed to the widespread increase in tree cover in some parts of tropical Africa [30]. Where megaherbivores persist, their distributions, densities, movements, and behaviours are seldom free of human impacts.

² This appears to invalidate the genus *Loxodonta*, though an accepted resolution has yet to be found at the time of writing.

The three largest surviving species of terrestrial megafauna are the elephants. The Bush elephant (*Loxodonta africana* Blumenbach, 1797) and the smaller Forest elephant (*L. cyclotis*) are restricted to continental Africa and were considered subspecies until recently [31, 32] but the genetic evidence for separation is unambiguous [33–35] and shows no significant interbreeding in the last half million years [19]. Both sexes of both species grow throughout their lives [7]. Adult bull Bush elephants can exceed six tonnes, with some accounts claiming over ten, while Forest elephants seldom exceed 3.5 tonnes [7]. The third species is the Asian elephant (*Elephas maximus* Linnaeus, 1758) which seldom reaches five tonnes [7].

Here, I shall focus on the African elephants. Both species have been heavily hunted – impacting their distributions, densities and behaviours [36, 37]. Despite these caveats, as Hempson and colleagues note [30], “Africa is effectively the world’s last laboratory for testing the effects of native large mammal herbivores on ecosystems”.

While the Bush elephant persists in scattered populations in a diversity of dry, seasonal and humid climates in sub-Saharan Africa, the Forest elephant has a more restricted distribution and occurs in a moist equatorial region including northern Congo, Gabon, the Central African Republic and southern Cameroon. Where they overlap the two species may mingle but seldom hybridise [38]. A frequent misunderstanding arises from the names of these animals, given that Bush elephants frequently use (and reside in) forests while Forest elephants often use, and spend considerable time in, non-forest habitats.

While all modern elephant species are generalised feeders – eating fruit, grasses, herbs and foliage when available – they are distinct from smaller browsers in their ability to utilise low quality fibrous and woody material too. This is consistent with theory which indicates that the largest animals can access and utilize foods that would be neither available nor nutritionally viable for smaller animals [39, 40]. Bush elephants (which are better studied) regularly consume bark, twigs and other woody material. These animals are also better able to gouge through thick bark, push down trees and dig up thick roots [41–43]. The proportion of woody material in their diet tends to be higher when alternatives are unavailable [42]. Woody material (primarily twigs and small branches ingested with foliage) can comprise over 90 % of food intake of elephants during the dry season in the arid woodlands of the Chobe National Park, Botswana [44]. Similar selection patterns (80 % woody material) have been seen in the dry season in wooded grassland of Tanzania’s Ruaha National Park [45]. The ability to eat low quality foods does not mean

elephants have low nutrient requirements or lack selectivity – rather they need to ingest nutrients at a greater rate than any other terrestrial mammal and choose the most nutritious foods they can [46]. Elephants derive sufficient nutrients from low quality foods only by consuming enormous quantities [47, 48]. Measured in dry matter, Bush elephants consume 1.0–1.6 percent of their body weight daily, while Asian elephants consume 1.5–1.9 percent [49]. Furthermore, while they ingest woody material, they do not seek wood, and wood alone lacks nutrients to sustain them. Indeed, while various organisms such as “white rot” Basidiomycota fungi, and several prokaryotes, metabolise and degrade lignin and lignocellulose, and this is also achieved by certain arthropods through microbial symbiosis [50, 51], we know of no vertebrates that derive significant energy from consuming wood.

Elephants and tree mortality

Gorshkov and Makarieva [1] are concerned with “megaherbivores”, meaning herbivores that reach over one tonne. As noted above, few such species remain, and Bush elephants are the largest among them. So, do these elephants kill trees and clear forests?

Bush elephants do contribute to tree mortality and loss. Observations in a large but fenced South African savanna park with artificial watering points (Kruger) found treefalls were six times more frequent in areas used (versus unused) by elephants [52, 53]. Long term studies show that these activities reduce tree cover (mean standing biomass declined by an estimated 87 % between 1998 and

2012 as elephant numbers grew after culling ceased in 1994) [54]. In contrast, a similar increase in elephants in Chobe (also savanna) was not associated with reduced tree cover, though wetter years and changes in fire regime have been proposed as explanations [54–56]. In the Serengeti’s equatorial savannas too, elephants contribute to tree mortality [57]. Various observations show that many trees are damaged or toppled without any feeding. Trees are sometimes pushed down in play or by an animal scratching itself (Fig. 2c). The reasons for this destructiveness remain unknown but social interactions appear to play a role [reviewed in 58].

In closed forests Bush elephants browse and trample saplings and seedlings (Fig. 1). They will often break the stems of small fruiting trees, such as *Myrianthus holstii* Engl., too [59]. Fredrick Ssali (my ex-student) followed 27 km of recent Bush elephant trails through the undergrowth of the Bwindi Impenetrable National Park (a mountain forest in Uganda). He found that the elephants knocked down 30.5 % of the stems over 2 cm diameter within 2 m of their temporary trails, tore branches from 19 % and stripped bark from 22 of 897 (mostly larger) tree stems [60]. Some pioneer species (the “weedier” trees that grow in disturbed areas) such as the fast growing *Macaranga kili-mandscharica* Pax were preferred while some other species were avoided. Damage rates were greater for stems in or near more open versus denser forest [60]. Studies elsewhere also show that Bush elephants preferentially feed in more open and disturbed forest where there is typically more accessible vegetation [61, 62].

Fig. 1. Camera trap images, from the Bwindi Impenetrable National Park (Uganda) of an African Bush elephant (*Loxodonta africana*). The animal (a) enters the frame and (b) feeds, before (c) turning to smell the camera, and (d) continuing to feed on saplings. All photographs by B. Mugerwa and D. Sheil, TEAM Network

Fig. 2. *a* – elephants depend on regular access to water and many of their impacts are greater near to favoured water access (here a heavily trampled access point in the Queen Elizabeth National Park, Uganda); *b* – a severely de-barked *Symphonia globulifera* L.f. tree in the Bwindi Impenetrable National Park (Uganda), with tusk marks visible up to 4 meters above the ground. Despite exuding a sticky yellow latex this species is often tusked; *c* – bush elephants often push down trees without feeding on them – here an animal is scratching itself against a fallen tree; *d*, *e* – several forest tree species have stem structures that prevent elephants from peeling off their bark, here two *Zanthoxylum* L. (likely both *Zanthoxylum gillettii* (De Wild.) P. G. Waterman) in Uganda – *Zanthoxylum* is a pantropical genus of about 200 species many of which bear similar structures on their stems. All photographs by D. Sheil

I have seen how Bush elephants damage large forest trees too – stripping bark and gouging stems (Fig. 2*b*). During my doctoral research in Uganda I found that most larger trees in the Rabongo Forest (a small remnant of old growth forest, regularly visited by Bush elephants from the surrounding Murchison Falls National Park) showed stem scarring from elephant tusks (more than half of stems over 50 cm diameter showed such damage) [63]. Ring-barking (removing bark all around the stem sometimes referred to as “girdling”) generally kills an impacted tree while less severe bark damage increases the likelihood of rot and reduced life expectancy [41, 42, 64, 65]. Though many animal species, including smaller taxa such as rabbits, voles, porcupines and beavers, along with deer and various primates, can cause such bark damage, and this causes significant local problems for forestry [66, 67], the wider ecological implications remain little studied. Indeed, I note that those who review causes of tree death in tropical forests generally

neglect such influences [e.g., 68]. Nonetheless, such damage is clearly influential in many locations and was, like the megaherbivores, likely more widespread and consequential in the past.

In my studies in Uganda, I found evidence for four strategies – repellence, resistance, tolerance and avoidance – that help trees coexist with elephants [63]. For example, strong repellence is found in species which possess toxins in their sap or bark, such as *Antiaris toxicaria* Lesch., *Strychnos mitis* S.Moore and *Erythrophleum suaveolens* (Guill. & Perr.) Brenan [63]. Repellence is also noted for *Holoptelea grandis* (Hutch.) Mildbr., a common forest edge species which emits a pungent “iodine like” smell when its bark is damaged [69 and DS pers. obs.]. All these species are left untouched by elephants [63]. Species with spiny stems such as *Dichrostachys cinerea* Wight & Arn., and species with spine like structures such as *Zanthoxylum gillettii* (De Wild.) P. G. Waterman also seemed resistant to bark stripping and were seldom damaged [Fig. 2*d,e*, 63].

Some tree species appear to tolerate, or perhaps even benefit from, elephants. A good example comes from Kenya's Shimba Hills National Reserve, a coastal forest where a high density of Bush elephant has been seen to browse on fast growing *Leptonychia usambarensis* K. Schum. trees that coppice and maintain the forest in a thicket-like early successional state [70].

Elephants do not push down larger rain forest trees (over 20 cm diameter) and there would be little benefit in doing so. The main large forest tree in the forests I know, *Cynometra alexandri* C. H. Wright, remains largely untouched by elephants, though the animals occasionally gouge the lower parts of the stem and buttresses. They would not be able to bring the larger trees down. The wood is dense, extremely tough, and contains hard mineral crystals that quickly blunt steel saws. In my doctoral work I speculated that the abundance of buttressed stems and species in these forests resulted from selection by elephants: buttresses not only increase stem stability but reduced the risk of ring barking and of rot reaching the heartwood [for more details, see 63]. The main impacts appear to be through damage to smaller stems. A decline in elephants results in the understorey becoming denser due to reduced damage and is likely one reason why some African forests have been gaining biomass over the last half century [71–74].

The Forest elephant is less destructive than the Bush elephant. It tramples and browses but seldom tusks or topples trees [75, 76]. Nonetheless, in forests used by these animals the density of saplings is negatively associated with local elephant densities [77]. They also, together with other large mammals, generate and maintain forest clearings – called “baï” across Central Africa – through their feeding, trampling and digging [78, 79]. The density of Forest elephants at, and around, forest edges is often higher, and sometimes much higher, than within the forest [76].

There are claims that Forest elephants ensure higher forest biomass than would otherwise occur. They supposedly favour large dense-timbered stems by selectively removing others with low density wood [80] – scepticism seems warranted, however, as the study neglects how these browsers favour and maintain open and disturbed vegetation, and results appear dependent on poorly justified model parameter values and the relationships among them. Relationships between timber densities and basal area in mixed species forests require further evaluation [suitable data exist, see, e.g., 81]. Others had long ago suggested that (Bush) elephants accelerate succession by preferentially impacting the regeneration of early successional species [82] (similar to the claim for Forest elephants

noted above though neglected by them [80]). I have seen this preferential removal of early successional species in my own observations too, but the implications are context specific; elephants can favour both late and early successional species and thus generate and maintain heterogeneity [63]. The consequences of their feeding favour early successional species when they feed preferentially in and create more open areas and keep them open thus encouraging and maintaining rapid growing light demanding species – as in the Shimba Hills example mentioned above [70]. However, they also favour late successional species when they seek out and preferentially reduce more palatable species in the shadier environments where the remaining less palatable species maintain sufficient shade to prevent regeneration of pioneer species. Indeed, given the life-histories available to evolving tree species, I have speculated that in the presence of elephants it appears better for a tree species to specialise in being either a damage-tolerant fast-growing pioneer or a repellent slow-growing but well-defended late successional species – both of which can be favoured in suitable conditions – rather than a generalist that is poor at both and is less able to persist. Similar trade-offs, selecting for alternative specialisations, have been indicated in other studies of plant defence with relation to herbaceous plants and insects [e.g., 83, 84]. The presence of such pressures against generalist behaviours by trees suggests not only that mid-successional species are especially vulnerable to elephants and other large herbivores, but that such herbivores have accentuated the evolved differences between pioneer and shade-tolerant tree species [63]. One testable implication is that mid-successional tree species will be less favoured when these animals are abundant than when they are scarce or absent [63].

So, elephants do kill trees. Bush elephants, in particular, are not limited by their appetites and often push down and damage trees without feeding. They have a major impact on savanna trees and modify the composition and structure of dense forests. Nonetheless, in the short term, not all tree species are vulnerable. Sustained trampling and damage could, over decades, prevent regeneration leading to larger trees not being replaced when they die (possibly aided by fire – see below). It would only be after this process was complete that elephants might “claim all ecosystem productivity” as Gorshkov and Makarieva [1] propose.

Population growth and constraints

Gorshkov and Makarieva [1] argue that megafauna lack the constraints on population growth

that govern smaller fauna. Curiously, Darwin also wrote about the geometric growth of elephant populations in *The Origin of Species*: he noted there “is no exception to the rule that every organic being naturally increases at so high a rate, that if not destroyed, the earth would soon be covered by the progeny of a single pair” [p. 64, 85]. This theme was widely repeated [see 86]. Such examples highlight the hypothetical power of unlimited growth – but reality differs.

Long-term studies have clarified the demography of elephants. Details vary with circumstances, but maximum population growth for Bush elephants has been estimated at around 7 % per year: doubling each decade in productive open habitats [87–89]. Demographic rates for Forest elephants appear lower though researchers have avoided offering an estimate due to challenges in interpreting their observations [90]. Even if 7 % per year is possible, can such growth rates be sustained? In nature we expect populations to approach some approximate equilibrium in which mortality and recruitment balance. So, what determines this balance for elephants?

The circumstances under which Bush elephants sustain healthy populations remain debated [e.g., 91]. Although they are flexible, eating diverse foods in numerous habitats, they require drinking water [Fig. 2a, 92, 93–95]. They do not always use the most accessible water [96], but prefer (or excavate) clean sources [97–99]. Our own observations in mountain forest landscapes indicate that elephants have less impact on forest areas farther away from favoured water sources [100].

Proboscideans are vulnerable to various health disorders. Both African elephant species are susceptible to various parasites which influence their fitness and survival [101–104]. Their viruses are little studied but do cause sporadic disease outbreaks and mortality [105, 106]. More is known about bacterial infections, such as tuberculosis *Mycobacterium tuberculosis* (Zopf), that have long been recognised to afflict these animals [107, 108]. The bones from many North American Mastodons (*Mammot americanum* Blumenbach) indicate tuberculosis – suggesting this disease contributed to their extinction [109]. The bones of the Eurasian Woolly mammoth also indicate frequent poor health, even among juveniles, though in this case dietary deficiencies have been suggested [110].

Water and disease are not the only influences. There is evidence that Bush elephant populations are constrained by food and fecundity [111–113]. Droughts not only restrict access to clean water but can also lead to starvation as animals aggregate around water and deplete available vegetation [114].

Predators also impact elephants [111, 113]. Bush elephants up to seven years old remain vulnerable to predation by lions (*Panthera leo* Linnaeus) [112, 113]. Younger juveniles are vulnerable to hyaena (*Crocuta* Erxleben) too and are especially vulnerable when animals must aggregate around limited water, as occurs during droughts [112, 113].

The giants of the past suffered predation too. Van Valkenburgh and colleagues [115] show that even the Pleistocene’s largest herbivores remained vulnerable to predation and drought. In brief, they show that juvenile mammoths and mastodons were vulnerable to felids and pack hunting canids (several of these carnivores being substantially larger than their present-day relatives).

Gorshkov and Makarieva [1] suggest that a “population of large animals can increase to a point when the animals will consume all young seedlings produced by mature trees”. While we lack clear evidence either way, it is doubtful that populations would grow, or even persist, once food was depleted – especially if it coincided with extended droughts, stress-related diseases, restricted water availability, and increased predation. There may be some lag in the density dependent dynamics, but such populations will decline. The question remains whether, and under what circumstances, such populations can nonetheless destroy enough forest to impact the climate and how such processes may advance.

Savannas in an evolutionary context

Gorshkov and Makarieva [1] note that the process of degradation that they predict from overstocking with herbivores “is described and studied for savannas”. In the next sections I review the interplay between savannas and tree cover, including forest, and the influence of herbivores. First, what is a “forest” and what is a “savanna”? Forests and savannas have both been defined in many ways that can make it hard to compare quantitative studies. Here, taking a broad approach, I consider forests as dense (closed or near closed) tree cover and savanna as tropical grasslands with scattered woody vegetation.

The expansion of savannas between 3 and 8 million years ago is poorly understood [116]. Most savanna grasses are C4 species adapted to open conditions and periodic drought [117–119]. Stable isotopes permit us to trace this vegetation through time [see 120, 121, 122]. This reveals that the global expansion was neither smooth nor simultaneous [123–125]. While hoofed ungulates are sometimes highlighted as central in the emergence of C4 savannas [e.g., 126], these biomes also ex-

panded into locations without such ungulates: for example, Australia with its marsupials [127] and Madagascar [128] where pygmy hippos and giant tortoises grazed [129, 130].

Savannas are one, comparatively recent, result of the long coevolution among plants, fires, and herbivores. Exploring these relationships into deep time offers evolutionary context. I start with fire.

The likelihood of wildfires is influenced by the levels of atmospheric oxygen and this has varied markedly over time [131]. Experiments show that if oxygen levels are below 13 %, wildfires will neither ignite nor spread irrespective of fuel moisture content. With oxygen levels between 13 and 16 % oxygen, only dry plant material can sustain a fire. Above 25 % oxygen fires would become widespread, even in wetter climates while at levels >35 % fires might not be extinguished [132]. As a result of these relationships, and their impact on carbon burial (see below), it is believed that fire played a role in determining levels of both atmospheric carbon dioxide and oxygen [132].

Evidence of fires occurs throughout the fossil record and often in abundance (charcoal and char-related material). Fire was present from the beginning: the first terrestrial plants (Silurian) and forests (Devonian) burned [132–134]. Multi-storied Devonian forests formed in wet habitats and were generally dominated by deep-rooted spore producing Archaeopterids (*Progymnospermopsida*). These are sometimes considered the first trees, with woody trunks and a height of over 30 m [135]. These forests sheltered a range of other organisms including climbing plants and arthropods, while their riverine channels sheltered not only a diverse range of freshwater fishes but also water dependent tetrapod vertebrates. Detailed studies in fossil materials from such forests reveals fragments of charcoal, some of which preserve anatomical structures suggesting they result from *Rhacophyton*, a shallow-rooted zygopterid fern [136]. As an aside, I note that the expansion of this terrestrial vegetation, with its impacts on weathering and increased nutrients entering the marine environments, may have contributed to the atmospheric changes that led to the late Devonian extinctions [134, 137].

Atmospheric oxygen peaked at around 35 % in the Permo-Carboniferous (~300 million years ago or “mya”) [138] facilitating gigantism in insects and coaxing vertebrates onto land. This was nonetheless a time of low atmospheric carbon, and extensive glaciation. Fires were widespread among the forests that thrived in wet environments [139, 140]. Trees reached 50 m tall and intermittent fires burned as high as the forest canopy [140, 141]. The common ancestor of modern conifers at this time appears to have been serotinous (i.e. not re-

leasing seeds without sufficient heat) – an adaptation to fire in modern ecosystems [142, 143]. Fossils suggest that plants in these forests developed other adaptations to fire such as the thick corky stem surfaces on the tree-like *Calamites* and lycopsids that charred rather than burned [138, 139]. The charred material that resulted from these burned forests contributed to coal formation. For example, most major coal deposits originate in the forests of the Westphalian 313–304 mya. Fusain, a compound resulting from the incomplete combustion of plant matter, comprises much of the carbon in these coals which is interpreted as a consequence of the repeated incomplete burning of these fire adapted forests [138]. (Limited ability to metabolise woody material may also have played a role. For example, molecular analyses suggest that the common ancestor of termites and the wood-digesting roach genus *Cryptocercus* separated more recently at about 170 mya [144]).

After the Permo-Carboniferous oxygen and fire peak, a subsequent decline in atmospheric oxygen reduced wildfires to much lower levels for over one-hundred million years [145]. The widespread loss of forests 305 mya heralded the end of coal formation, and the start of a drier era with more fragmented vegetation which greatly influenced the diversification of surviving tetrapods (early amphibians and reptiles) [146]. Fires and fire ecologies flourished again 140 mya when oxygen levels reached 28 % making the mid-Cretaceous “one of the most flammable periods in the Earth’s history” [145]. Many adaptations seen in modern plants, such as fire dependent seed release and germination, evolved at that time [145, 147]. Furthermore, many modern vegetation types are both flammable and adapted to fire [148, 149]. So, how does this compare with herbivory?

Like fire, herbivory by large vertebrates can also be assessed from fossil evidence. Terrestrial megaherbivores have likely included browsers since Gondwana’s Permian glossopterid forests supported large dinocephalian and anomodont therapsids over 250 million years ago [150] but the evolutionary and ecological implications remain hard to discern in the fossil record. Studies of skull shape, dentition and tooth wear can help distinguish grazers from browsers among therapsids, dinosaurs and other taxa [151, 152]. Occasionally stomach contents or coprolites preserve sufficient structure to further indicate that these ancient giants ingested woody material, but interpretation remains contentious and provides little insight into the prevalence and significance of browsing [153–155]. In one unusually well-preserved example, twig fragments “likely from conifers belonging to the Cupressaceae or Taxodiaceae” were found in

Montana USA, in fossilised droppings attributed to the two-tonne hadrosaurs (*Maiasaura peeblesorum* Horner & Makela) from 74–80 mya. Even in this example, the authors remained uncertain if the woody material derived from live or dead trees [154].

How did plants respond to herbivory? In the current era we see plants producing phytoliths, resins, stings, irritant hairs, trichomes, sticky latex, spines, thorns, prickles, glochids, other spinose structures, or by thigmonasty/seismonasty (response to touch), association with ants, mimicry, camouflage or the manufacture, and/or accumulation, of chemical defences that inhibit digestion, reduce palatability, and/or are toxic (phenolics, alkaloids, terpenoids, metal ions, etc.). There are also defences that involve mechanical strength, toughness and resistance to damage, and strategies that involve plant architectures that obstruct access. Few such defences can be inferred confidently from fossils. An exception is the woody spines which have been observed since the Triassic [156].

What preceded modern savannas? We know little about the ecology of the open Paleogene environments and their faunas [for a review, see 157]. A phylogenetic investigation into spiny vegetation in Africa suggests browsers maintained open vegetation millions of years before modern grassy savannas existed [158]. What about the understorey? Coe and colleagues [159] speculated that "fern prairies" supported grazing dinosaurs in the Mesozoic. This seems consistent with modern-day ferns that maintain persistent clearings in both tropical and temperate forests [160–162]. For example, like many forests worldwide, Bwindi, Uganda, has extensive clearings supporting bracken fern *Pteridium aquilinum* (L.) Kuhn [some persisting > 40 years, 163]. Few animals eat this fern at Bwindi, though Bush elephants (and occasionally also bush pigs *Potamochoerus larvatus* F. Cuvier) appear exceptions: according to local people the elephants hold the fronds with their trunks and then, by swinging their front leg from side to side, slice the rhizomes from the ground using their toenails. This leaves extensive areas of open soil that are soon recolonised by bracken [100]. Our data show that few tree seeds manage to reach, germinate and establish in these fern-dominated areas [164, 165], and those seedlings that establish, even if not sought out as food, have an estimated 61 % chance of severe damage each year due largely to the activities of animals [100]. While elephants help maintain these clearings, they are not essential, and extensive and persistent bracken patches also occur without elephants, for example, in Nyungwe Forest (Rwanda), which has suffered recurrent fires [166].

The initial spread of Africa's C4 grasses, assumed to be the birth of the savannas, coincides with the instabilities of the "Messinian Event" 6.0–5.3 mya – when the Mediterranean dried up repeatedly and the world's oceans became less saline paving the way for the subsequent glacials [167, 168]. Savanna expansions had various consequences [see, e.g., 169]. The influence of smoke (and related emissions) from frequent grassfires on rain and lightning (potential ignitions) remains uncertain, but less forest and more grass will generally increase the likelihood of fires that favour savanna thus entailing a positive feedback [126, 170]. Any regional decline in tree cover reduces rainfall, increasing the likelihood of fire and further forest loss. If we couple this idea with more recent insights into the powerful feedbacks maintaining wet climates within continents there is no doubt that forest loss will disrupt the climate and ultimately risks tipping whole regions from wet to arid [2, 171–173].

There are global feedbacks too. For example, savanna expansion (perhaps counterintuitively, as I explain below) reduces atmospheric carbon dioxide and increases atmospheric oxygen and thus boosts the worldwide likelihood of fires [126, 138, 174]. Such expansions, when combined with other changes such as reduced ocean salinity and orbital shifts [175], led into the unstable Pleistocene – with extended arid glaciations, sea level changes, fluctuating atmospheric carbon dioxide and shifting vegetation [176–179].

How do vegetation fires influence atmospheric composition? Over geological time scales atmospheric oxygen levels are modified by the global carbon and sulphur cycles – for a fuller account see Berner and colleagues [138]. Briefly here focusing on the carbon aspect, vegetation fires enhance sequestration of carbon from the atmosphere through the creation and accumulation of charred pyrogenic material in the soil as this is more resilient to breakdown than other plant-derived organic matter [174]. So, while any individual fire will reduce oxygen and increase carbon-dioxide, frequent fires can lead to carbon being removed from the atmosphere and buried – as seen in the formation of the carboniferous coals mentioned above. While this mechanism has been neglected in models of the global carbon cycle there have been recent calls for this to change [180]. While various other processes such as weathering play a role too, there is good evidence of a positive feedback where higher oxygen leads to more fires and more charcoal production and burial further increases oxygen [138, 181].

Generally, forest retreat is considered a consequence of the glaciations. Yet, feedbacks between atmospheric moisture and circulation suggest that

changes in forest cover could be influential in determining latitudinal temperature gradients too [182–184]. In this context, any regional change in the dynamics between tree cover and other vegetation would be important and could help explain why vegetation change often varied among sites and periods [178, 185, 186]. Unfortunately, we lack the data needed to characterise these relationships across the tropics. Furthermore, we see elsewhere that even when good data are available, detailed interpretation remains challenging [e.g., 187, 188, 189].

Savanna-forest dynamics

Savanna-forest dynamics have been extensively studied. Yet, as Hoffmann and colleagues [190] note “there is no consensus regarding the relative importance of climate, fire, hydrology, herbivory and soil characteristics in mediating the balance

between these biomes”. Observations from tropical Africa show that closed forests can occur with as little as 700 mm of annual rain – but nonetheless tree cover often remains scattered and open even in much wetter sites [Fig. 3a, 191]. As I shall examine in this section, such open vegetation is often attributed to fire (the role of animals is examined in the subsequent section). While savanna and forest are sometimes considered alternative stable states [192], this label is somewhat misleading as savanna tree cover, rather than being stable, appears in constant flux [193]. Local investigations show that site conditions are influential (e.g., soil moisture, termite activity and access to grazers, Fig. 3b). Nonetheless, fire appears key. Fire is not choosy about nutritional attributes and has a vastly larger appetite than any herbivore. According to one simplified simulation, without fire global tree cover would double [see 194].

Fig. 3. *a* – woody cover versus annual rainfall, based on 854 sites across Africa and redrawn from Sankaran, Hanan [191] showing a 99th quantile piecewise linear regression. Trees are absent below 100 mm rainfall, and the maximum cover rises markedly between 100 and 650 mm, but most sites achieve a woody cover that is well below the maximum; *b* – our work in Lake Mburu National Park, Uganda, (mean annual temperature and rainfall: 20.7°C and 865 mm) suggests that tree cover in this landscape is increasing, a process that is facilitated by the presence of termite mounds as well as by fencing – as in this image – that excludes large herbivores [but not fire, see, e.g., 265]. Photograph by D. Sheil

Savanna grasses possess characteristics – e.g., rhizomes and protected meristems – that tolerate recurrent grazing and fires [126, 195]. Grasses evolved to be flammable. The rapid growth and slow decomposition of savanna grasses fuel fires that can suppress the regeneration of trees.

While many details about the evolution of flammability as an adaptive trait remain debated [148, 196–198] there are various modern day species, and indeed biomes, that are not only flammable but depend directly or indirectly on fire [199]. The question of how flammability is selected is made more complex by indications that

there may be more than two – flammable versus non flammable – strategies [149]. In any case, some model-based results suggest flammability can be selected for when feedbacks favour the expansion of flammable species from more fire-prone into less fire-prone areas [200]. In addition, recent theory suggests flammability can be selected for under certain conditions including the delayed succession that can result from more frequent fires [201].

Mature savanna trees typically possess thick fire-resistant bark [202, 203] – but saplings remain thin barked and vulnerable, and they take time to

grow large enough to survive fire. Frequent fires mean the above-ground parts of small and still-vulnerable stems are killed [190, 204]. Successful tree recruitment requires sufficient time between fires for saplings to reach less vulnerable dimensions [205]. Tree cover, in contrast to grass, typically reduces fires (e.g., through increased shade and moisture, and reduced wind) and thus favours the recruitment of more trees. Once tree cover becomes dense enough fires become less likely. Observations in Southern Africa show that fire frequency declines markedly once tree cover exceeds 40 % [206]. If tree cover is maintained, and the necessary seeds and diaspores are present, a dense woodland composed of savanna trees can develop into a closed canopy forest. Such successional developments can take decades or centuries [72, 207, 208].

Typical forest trees are specialised to establish and compete in shady forests: most are thin-barked and sensitive to fire even when mature [202, 203, 209]. Once they are established, most broad-leaved tropical forests are damp places that do not readily burn. Nonetheless, a usually non-flammable forest can become flammable following extended droughts – such events can kill larger trees and favour the accumulation of dry litter that can fuel fires and kill small trees [something I have seen in Borneo, see 209]. Such fires tend to kill many stems, opening the canopy, thus generating the fuel and lower humidity that increases vulnerability to, and thus the likelihood of, future fires [210].

The frequency and significance of fire in wet tropical forest prior to human presence is uncertain. We do know that such fires are almost always associated with droughts that allow dead biomass to become flammable. There have certainly been droughts and fires in otherwise wet forests before extensive human impacts. An explorer who visited Borneo in 1879 (before extensive forest loss) reported a drought that lasted over eight months, leaving a third of forest trees dead [Bock 1881 quoted in 211]. There is also evidence of fires going back at least ten thousand years [212]. However, modern humans have been active in Borneo for at least fifty thousand years [213] and their impacts may be greater than has been generally assumed [214]. If we want to look at continental forests prior to any human impacts, we turn to Amazonia: unfortunately, the evidence here is inconclusive. Charcoal in Amazonian soils have been dated back to over nine thousand years ago but can still be interpreted as having human origins [e.g., 215]. Some site-based studies show no sign of fire over many centuries despite human presence [e.g., 216]. Lake sediment cores reveal at least some charcoal particles arriving up to fifty thousand years ago

(before humans arrived) but the sources remain uncertain [217]. What is widely accepted is that human activities greatly increased the likelihood of forest fires [210]. There is also increasing awareness that such fires can, through multiple mechanisms (relating to reduced humidity, less reliable rain and increased and more frequent availability of flammable fuel) enhance the likelihood of subsequent droughts and fires [2, 172, 218–220].

In the long term, systems can switch between states, forest or non-forest, depending on details of the fire regime [190, 205]. Outcomes depend on conditions during the brief period of fire ignition, combustion and contagion (spread). Ignition appears the least understood.

Prior to human activities, ignition had to arise naturally. There have been various suggestions how this can occur: lightning strikes, spontaneous ignition within composting biomass, concentrated sunlight, sparks (e.g. generated by rock-falls, or animals), friction (e.g. tree stems grinding against each other in wind), volcanic activity, meteorites, and various chemical processes (such as combustion of phosphines [221]). The plausibility and significance of these are uncertain, but lightning is generally judged the dominant (but not sole) cause of ignition in natural systems [222–224]. There are also situations, such as when coal (or peat) seams include openings to air and can ignite spontaneously (or from external fires) [225] and can smoulder in protected conditions for many years and re-establish vegetation fires when conditions permit [212]. Such sustained underground fires have become important in the modern world where roads, mines and related developments have exposed coal. For example, in Indonesia in 1998 it was estimated that 250,000 distinct fires remained burning in subterranean coal seams [225] and were difficult to extinguish [226, 227]. Whether or not ignition events limit the frequency of fires in any location depends also on the scale of the subsequent fires, which is determined by their ability to spread. While the determinants of savanna in a pre-human world remain uncertain, there is little doubt that, along with fire, animals played a significant role.

Animal influences

Vertebrates can influence the balance between trees and grass in many ways [see, e.g., 228, 229–231]. For example, as Gorshkov and Makarieva [1] also note, rodents may remove tree seeds and impede forest establishment. Seed rain far from trees is often low and seed removal rates high [232]. Pigs sometimes achieve high densities and threaten forest regeneration and recovery – though these effects are often transient [233–235]. Sustained

browsing by abundant antelopes can hinder tree establishment in savannas [236]. Animals can influence the quantities, structure and condition of potential fuel for fires – and thus influence the nature, likelihood, frequency and spatial scale of fires [231]. Animals may even use and spread fire: observations in Northern Australia show that kites and other raptors sometimes seek smouldering sticks (from bush fires or human hearths) and carry them to purposefully start fires elsewhere as a means to flush out prey [237]. Similar claims are known from Africa, Asia and the Americas [M. Bonta quoted in 238].

What about more typical animal behaviours? Browsing generally reduces woody growth and the likelihood that small trees escape fire [239–241]. Grazing generally reduces competition from grass, as well as fire intensity and frequency [231, 242], and thus favours tree establishment [229, 230]. Fluctuations in vertebrate grazers, e.g., following disease or drought, can have a marked impact on tree recruitment [243, 244]. One argument against a particular importance for megaherbivores is the similarity in apparent tree density patterns in Africa (with megaherbivores) and Australia (without) [245, 246] though anthropogenic influences may also explain this convergence. As Johnson and colleagues note [228] “our knowledge of the effects of vertebrates on fire is still sparse, as well as being unevenly distributed in geographical and environmental space”. Archibald and colleagues [247] are more pessimistic noting that “most savannas globally have lost much of their mammalian fauna”. In support of this view, modern day trees possess defences – such as spine-like protuberances high on large stems of various species including *Ceiba pentandra* (L.) Gaertn. and *Zanthoxylum gillettii* (De Wild.) P. G. Waterman (Fig. 2d,e) – that appear superfluous without megaherbivores.

The ability of fire to spread depends on the continuity of fuel, and the ability of the fire to cross gaps (e.g. by throwing embers). This is also important where biomes meet. For example, the activity of animals on forest-savanna boundaries can influence permeability to fire and whether the savanna or forest advance at the expense of the other. I have seen the processes operating in both directions in Uganda. For example, in Budongo Forest, low dense evergreen vegetation (*Acanthus* spp. etc) generally borders the forest and appears to be a barrier to fire. This forest has expanded over recent centuries [72, 207, 248]. Rabongo Forest, in contrast, is contracting as tree cover is lost at its edges. Large relic forest trees occur in the surrounding savanna, outside the current forest, while charring can be seen on tree boles within the forest [DS

pers. obs., 95]. Bush elephants and buffalos are especially active at Rabongo: the forest canopy is more open than in Budongo (likely due to limited regeneration), allowing a less humid understorey with a patchy vegetation at the forest edge and litter that sometimes dries out and permits fire to enter. In Gabon, Forest elephants are said to trample forest edges creating firebreaks [76], though whether this boundary is static or “natural” is uncertain (one common fruiting species attracting these animals is guava, *Psidium guineense* Sw., a naturalised alien species that favours forest edges [76]).

Conservation comments

A clarification is needed. Sometimes conservationists highlight what they consider the implied “positive role” of certain organisms to argue for their conservation. This may give the impression that giving credence and emphasis to “destructive roles”, for example, to megafauna reducing forest cover, is unsupportive. For that reason, I underline that I support both objective science (free of normative labels) and conservation (led by shared norms). I should also underline that forests are not the only biome requiring conservation: many savannas along with many other non-forest formations maintain important biodiversity and require protection. Regardless of how we view any ecological impacts of megafauna, the need for their conservation remains real and urgent. Furthermore, it remains true that elephants and other megaherbivores generate, maintain and modify the environments, habitat features and processes on which many other species depend.

As we have already seen, by maintaining open habitats elephants and other megaherbivores benefit the organisms that require these conditions, but they have significant additional influences too. They excavate and maintain pools that provide water in areas and seasons when water is otherwise unavailable [99]. They can influence the availability of key nutrients [249]. They may dig for access to salt, or modify land-surfaces and waterways [250]. They can impact the vegetation so as to facilitate other herbivores too [40, 251]. There are also plants considered dependent on elephants or other large animals for effective seed dispersal [252–255]. Such relationships are not limited to elephants or even the tropics [256, 257]. The relevance of these additional relationships for tree cover, and related feedbacks, remains largely unknown. Whatever the past implications, the risks we now face are almost exclusively of our own making: the world’s remaining megaherbivores must be valued and protected.

Synthesis

I agree with Gorshkov and Makarieva [1] that forests play a key role in stabilising the conditions of our planet. It is important to understand any threats to this stability, especially the conditions where positive feedbacks dominate. These are the “tipping points” where a small change has dramatic consequences [258, 259]. Some feedbacks operate at regional to continental scales [260] – for example, forest loss causing desiccation in Australia [261, 262], or tipping the Amazon from wet to dry [263]. Other feedbacks are potentially global, such as when rising atmospheric carbon dioxide promotes the release of additional carbon into the atmosphere [264]. While we know such feedbacks exist and are potentially powerful, our proximity to such tipping points in the past is less clear. The extent to which megaherbivores might reduce forests, or modify their hydrological influences, is also unclear. Observations of Bush elephants suggest that they can reduce tree cover and help maintain more open habitats that may also yield more elephant food and thus permit population growth. Furthermore, there are situations, as seen with persistent clearings, where forest is slow to recover, and impacts will accumulate while losses outpace recovery.

It is plausible that there have been periods when forest loss contributed to, or even determined, climatic instability and that megaherbivores influenced these dynamics. The Pleistocene glaciations coincide with extended periods of forest retreat, and of expanded aridity in Africa and elsewhere, and megaherbivores may have been influential. The wider role of megaherbivores in a world prior to humans remains difficult to infer when viewed from within a world bearing nearly eight billion people. There are plenty of uncertainties and unanswered questions, along with scope for speculation. Nonetheless, the overall story seems more complex than Gorshkov and Makarieva [1] imply. Rather than highlighting megaherbivores alone, I would point to fire and flammable biomes as warranting additional scrutiny (savanna, grasslands and various seasonal forests). When fire is involved, body-size becomes less fundamental – consider the potential impact of one ape with matches or a fire-carrying kite [237]. Furthermore, whatever conclusions may be reached, nothing in these discussions argues against the real and urgent need for conservation of the world’s remaining megaherbivores.

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