

Are hippos Africa's most influential megaherbivore? A review of ecosystem engineering by the semi-aquatic common hippopotamus

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ABSTRACT

Megaherbivores perform vital ecosystem engineering roles, and have their last remaining stronghold in Africa. Of Africa's remaining megaherbivores, the common hippopotamus (*Hippopotamus amphibius*) has received the least scientific and conservation attention, despite how influential their ecosystem engineering activities appear to be. Given the potentially crucial ecosystem engineering influence of hippos, as well as mounting conservation concerns threatening their long-term persistence, a review of the evidence for hippos being ecosystem engineers, and the effects of their engineering, is both timely and necessary. In this review, we assess, (i) aspects of hippo biology that underlie their unique ecosystem engineering potential; (ii) evaluate hippo ecological impacts in terrestrial and aquatic environments; (iii) compare the ecosystem engineering influence of hippos to other extant African megaherbivores; (iv) evaluate factors most critical to hippo conservation and ecosystem engineering; and (v) highlight future research directions and challenges that may yield new insights into the ecological role of hippos, and of megaherbivores more broadly. We find that a variety of key life-history traits determine the hippo's unique influence, including their semi-aquatic lifestyle, large body size, specialised gut anatomy, muzzle structure, small and partially webbed feet, and highly gregarious nature. On land, hippos create grazing lawns that contain distinct plant communities and alter fire spatial extent, which shapes woody plant demographics and might assist in maintaining fire-sensitive riverine vegetation. In water, hippos deposit nutrient-rich dung, stimulating aquatic food chains and altering water chemistry and quality, impacting a host of different organisms. Hippo trampling and wallowing alters geomorphological processes, widening riverbanks, creating new river channels, and forming gullies along well-utilised hippo paths. Taken together, we propose that these myriad impacts combine to make hippos Africa's most influential megaherbivore, specifically because of the high diversity and intensity of their ecological impacts compared with other megaherbivores, and because of their unique capacity to transfer nutrients across ecosystem boundaries, enriching both terrestrial and aquatic ecosystems. Nonetheless, water pollution and extraction for agriculture and industry, erratic rainfall patterns and human–hippo conflict, threaten hippo ecosystem engineering and persistence. Therefore, we encourage greater consideration of the unique role of hippos as ecosystem engineers when considering the functional importance of megafauna in African ecosystems, and increased attention to declining hippo habitat and populations, which if unchecked could change the way in which many African ecosystems function.

Key words: aquatic biodiversity, conservation, *Hippopotamus amphibius*, megagrazer, transboundary nutrient cycling, savannas, megafauna.

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I. INTRODUCTION

Modification of the physical environment by animals is a key ecological process. When such modifications are large enough that environmental changes are long lasting and affect other organisms, the species responsible for such modifications, or physical state changes, are referred to as ecosystem engineers (Wright & Jones, 2006). Through altering environments, ecosystem engineers not only regulate available resources, but also modify, maintain and create habitats for other species (Jones, Lawton & Shachak, 1994, 1997). However, we are only beginning to understand fully how such animals influence Earth ecosystem functioning (Malhi *et al.*, 2016; Hyvarinen *et al.*, 2021). Advancement in our understanding of animal impacts is hindered because many of the world's largest herbivores – among the most influential ecosystem engineers – are already extinct, or exist in low numbers in isolated and fragmented populations (Ripple *et al.*, 2015; Atwood *et al.*, 2020). Yet, where they still occur, they have large impacts and continue to shape present-day ecosystems. Moreover, 'ghosts' of ecosystem engineers past continue to affect contemporary landscapes and by studying extant engineering species we stand to gain valuable insights into these legacy effects and how they continue to affect current-day ecosystem functioning (Frauendorf *et al.*, 2021; Albertson *et al.*, 2022).

Large herbivores fulfil a particularly important role as ecosystem engineers, modifying their surroundings in distinct and profound ways that promote diversity (Owen-Smith, 1987; Zimov *et al.*, 1995; Gill, 2014; Malhi *et al.*, 2016; Hyvarinen *et al.*, 2021). Owing to their large body size (>1000 kg), megaherbivores are mostly immune to non-human predation (Owen-Smith, 1988), resulting in their populations being maintained closer to limits imposed by vegetation (i.e. bottom-up limited) than smaller herbivores that are subject to predation and often top-down limited (Owen-Smith, 1988). Megaherbivores have extensive impacts on vegetation structure due to their consumption of large amounts of vegetation (Cromsigt & Te Beest, 2014; Guldmond, Purdon & van Aarde, 2017), thereby shaping habitat for themselves and a variety of other species (Pringle, 2008; Le Roux, Kerley & Cromsigt, 2018). Megaherbivores are also capable of roaming over vast distances (Purdon *et al.*, 2018), rendering them especially important for maintaining and regulating spatially expansive ecological

processes, such as long-range seed dispersal (Bunney, Bond & Henley, 2017), and nutrient cycling (Doughty *et al.*, 2016). Advancing our understanding of megaherbivore impacts is critical for understanding the role of animals in shaping ecosystem functioning in both present-day ecosystems and where megaherbivores have gone extinct (Malhi *et al.*, 2016; Hyvarinen *et al.*, 2021), and even for understanding the human evolutionary trajectory (Faith *et al.*, 2018; Faith, Rowan & Du, 2019; Owen-Smith, 2021).

Well over 50 megaherbivore species are known to have existed until the late Pleistocene, distributed across all continents other than Antarctica. Today, only 13 species remain, with nine of these occurring in Africa (Malhi *et al.*, 2016). Most megaherbivore species, and a variety of other terrestrial mammals, are thought to have met a sudden demise at the end of the late Pleistocene, approximately 11,000 years ago (Owen-Smith, 1989). Explaining this global megafauna collapse has been a topic of considerable debate, with the prevailing view being that hunting by early humans led to a rapid, global megaherbivore decline (Lyons, Smith & Brown, 2004; Zuo, Smith & Charnov, 2013; Smith *et al.*, 2018; Bradshaw *et al.*, 2021), which is thought to have precipitated declines in smaller mammal species (Owen-Smith, 1987). However, recent evidence also suggests that globally decreasing atmospheric CO₂, beginning long before human arrival (~4.6 million years ago), promoted C₄ grasses over C₃ woody plants, leading to grassland expansion and consequent declines in megabrowsers (Faith *et al.*, 2018, 2019).

Late Pleistocene extinctions aside, there remains little debate as to the factors responsible for continued contemporary declines in large mammal populations (Ripple *et al.*, 2014, 2015) with humans undoubtedly playing a central role. The pervasive nature of exploitative hunting and land use change by encroaching human societies into previously natural areas has taken an immense toll on wildlife, especially for species that are large and long-lived (Ripple *et al.*, 2015, 2017; Atwood *et al.*, 2020). Given the ecological importance of megaherbivores and their historic and ongoing declines, there is an urgent need to advance our understanding of how megafauna impact ecosystems to anticipate the consequences of further megafauna loss. Furthermore, the current rewilding movement is resulting in the reestablishment of megaherbivore populations in select areas across the globe (Malhi *et al.*, 2016; Svenning *et al.*, 2016), with a subsequent need to understand how such reintroductions might alter ecosystems.

One prominent, yet relatively understudied megaherbivore is the common hippopotamus (*Hippopotamus amphibius*, hereafter hippo), the fifth-largest living land mammal after the three elephant species and the white rhinoceros *Ceratotherium simum* (Owen-Smith, 1988). Multiple hippo species have existed since approximately 11–15 million years ago (Mya) where they are first known from East African fossil records, and later throughout Africa, and parts of Europe and Asia (Eltringham, 1999). Today, only two extant species remain, the pygmy hippo *Hexaprotodon liberiensis*, a much smaller species restricted to isolated forest fragments in West Africa (Robinson, Flacke & Hentschel, 2017), and the common hippo, a water-dependent megaherbivore still occupying many of Africa's major waterways (Lewison & Pluháček, 2017). Yet despite the ubiquity of hippos historically, and their continued relative abundance in some parts of Africa (Fig. 1), hippos are poorly represented in the scientific literature and are arguably one of the least understood extant megaherbivore species (Hyvarinen *et al.*, 2021). Their semi-aquatic life history – a relic of their distant ancestry with cetaceans (Geisler & Theodor, 2009; Boissier *et al.*, 2011) – nocturnal grazing habits, and notoriously dangerous disposition (Utete, 2020), make them particularly challenging to study, perhaps contributing to hippos often being

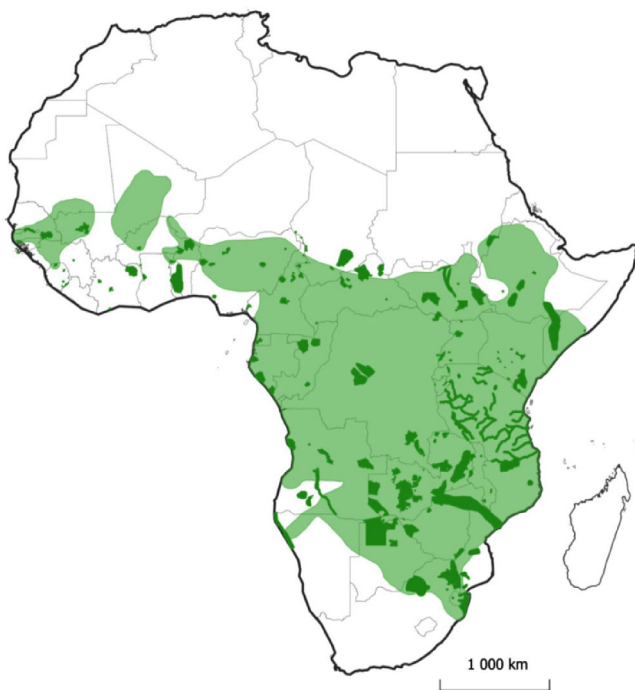


Fig. 1. Map of current (2017; dark green) and past (~1959; light green) common hippopotamus (*Hippopotamus amphibius*) distribution within sub-Saharan Africa based on the best available information from the International Union for Conservation of Nature (IUCN), adapted from Lewison (2007) and Lewison & Pluháček (2017). Before 1959, hippos are thought to have been found everywhere south of the Sahara in suitable habitat.

overlooked when considering the ecosystem influences of megaherbivores (Owen-Smith, 1989; Hyvarinen *et al.*, 2021).

Indeed, surprisingly little empirical evidence, from only a few studies, exists to support the claim that hippos play an integral role in the functioning of terrestrial and aquatic ecosystems (Fig. 2). Given this lack of insight, together with a declining global population (listed as vulnerable by the IUCN; Lewison & Pluháček, 2017) and ongoing range contraction from human-driven hydrological changes, habitat degradation, poaching for bushmeat, an expanding ivory market, and increasing drought frequency and severity (Zisadza *et al.*, 2010; Ripple *et al.*, 2015; Eksteen *et al.*, 2016; Andersson & Gibson, 2017; Stears *et al.*, 2018; Smit *et al.*, 2020; Utete, 2020), a review of the unique ecosystem engineering role of hippos is both timely and necessary. Here, we evaluate the evidence for hippos to be considered ecosystem engineers and assess whether their impacts are more consequential than those of other megaherbivores. In addition, we evaluate major conservation threats facing hippos and their potential ecosystem engineering behaviour. Specifically, we (i) assess aspects of hippo biology and ecology that constitute their unique ecosystem engineering potential; (ii) evaluate impacts that hippos have in both terrestrial and aquatic environments; (iii) compare the ecosystem engineering influence of hippos to that of other extant megaherbivores; (iv) evaluate the factors most critical to hippo conservation and persistence; and (v) highlight future research directions and challenges that may yield new insights into the ecological roles of hippos, and of megaherbivores more broadly, as well as assist in hippo management and conservation in an era of rapid global change.

II. THE MAKING OF AN ECOSYSTEM ENGINEER: THE CASE FOR HIPPOS

Ecosystem engineering impacts are exerted in accordance with the body size, behaviour, and abundance of the engineering species (Jones *et al.*, 1994; Moore, 2006). Hippos are considered important ecosystem engineers in African landscapes, because their large body size necessitates the consumption of substantial quantities of grass, thereby altering ecosystem processes such as fire regimes and nutrient transport. Hippos are also central place foragers (Lewison & Carter, 2004), making routine visits between grazing grounds and their aquatic habitat, spending most of the daytime wallowing, which can lead to considerable geomorphological change (McCarthy, Ellery & Bloem, 1998a; Bakker *et al.*, 2016), profoundly altering the environment and impacting a host of co-occurring species (Mosepele *et al.*, 2009). Moreover, hippos often congregate in large numbers (Fig. 3A) (Chomba, Simpamba & Nyirenda, 2013; Dutton *et al.*, 2018b; Stears *et al.*, 2018; Fritsch, Plebani & Downs, 2022), extenuating and amplifying their individual engineering impacts.

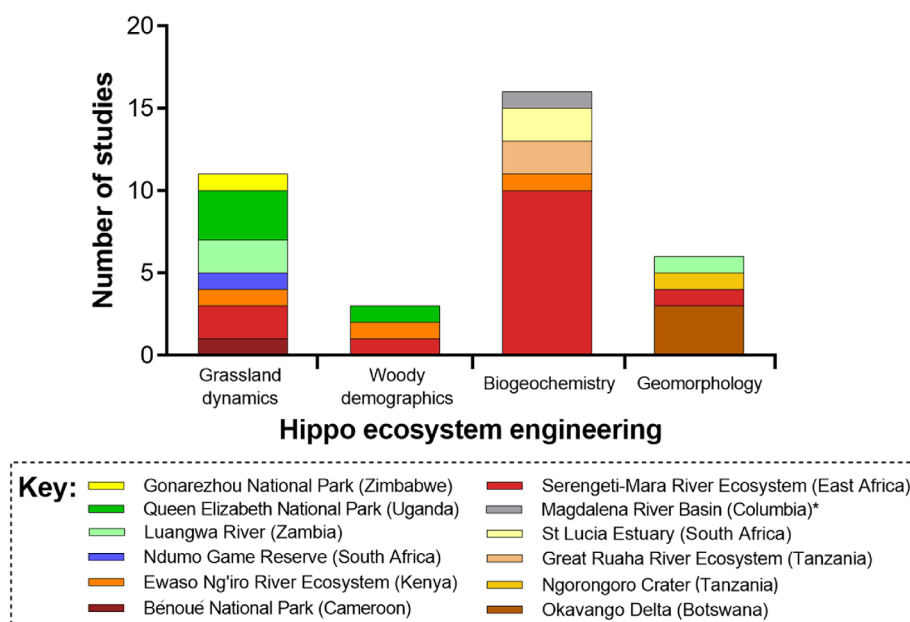


Fig. 2. The number of studies investigating hippo ecosystem engineering impacts. The reported studies are separated first into different themes of hippo ecosystem engineering (i.e. grassland dynamics, woody demographics, biogeochemistry, and geomorphology), and then according to the geographical location of the specific study area. An asterisk (*) indicates study locations that occur outside of the hippo's natural distribution. A search of the relevant scientific literature was conducted using *Web of Science* on 8th June 2022.

Adult hippos are large, routinely exceeding 1000 kg in body mass. During a culling operation of 2994 hippos between 1961 and 1966 in Queen Elizabeth National Park, Uganda, mean body mass for male and female hippos was 1393 and 1332 kg, respectively, with males being only 5% heavier than females on average (Shannon *et al.*, 2021). In Kruger National Park, South Africa, a culling operation of 104 hippos along the Letaba River yielded a mean body mass for male and female hippos of 1492 and 1325 kg, respectively (Pienaar, van Wyk & Fairall, 1966). The maximum mass of individuals from both sexes has been recorded at over 2000 kg (Bere, 1959; Pienaar *et al.*, 1966; Shannon *et al.*, 2021).

Hippo diet consists primarily of grasses, but dicotyledonous plants (forbs and woody seedlings) are occasionally ingested. Aquatic vegetation is avoided, and only eaten during times of extreme food shortage (Mugangu & Hunter, 1992). Fruits are not actively pursued, although *Faidherbia albida* pods were shown to contribute 1.9% of hippo faecal mass in samples collected along the Zambezi River (Dunham, 1990), and sausage tree (*Kigelia africana*) fruits (Fig. 3D) were found in seven out of 10 hippo stomachs in Zambia (Ansell, 1965; Namah, Midgley & Kruger, 2019). Carnivory by hippos has also been reported occasionally, mostly by scavenging as opposed to direct predation (Dudley *et al.*, 2016), suggesting that opportunistic sources of meat could provide nutritional supplements when vegetation is scarce or of low nutritional value (Eltringham, 1999).

Hippos graze using their lips, in a similar way to the white rhinoceros (Eltringham, 1999). During grazing, hippos

typically sway their heads in a side-to-side motion, plucking grasses as their lips come into close contact with the ground. Tall, tussock-forming grasses are not suitable for grazing in this manner, and are typically avoided, with this grazing technique best suited for short, lawn-forming grass species, resulting in the formation and maintenance of hippo grazing lawns (Verweij *et al.*, 2006). Their broad muzzle, reaching up to 50 cm in width, enables cropping of enough short grass to meet their nutritional requirements (Eltringham, 1999), but results in them being area-rather than species-selective grazers (Scotcher, Stewart & Breen, 1978). The hippo diet comprises a variety of grasses, most of which are short-statured species (Field, 1970; Verweij *et al.*, 2006; Olivier & Laurie, 1974a). Their grazing style, combined with the relatively large spatial extent of their grazing, results in hippos engineering entire plant communities, altering both the structure and species composition of savanna grasslands (Fig. 3B,C).

Hippo dung and urine scattering, which is done by rapid, side-to-side flicking of their tail (Fig. 3K), is an important aspect of hippo social biology. While some studies suggest that only males perform dung and urine scattering (Olivier & Laurie, 1974b), others have recorded this behaviour in both sexes (Estes, 2012). Females and sub-adult males scatter dung and urine when approached by dominant males, presumably as an act of subordination (Estes, 2012). By contrast, males scatter dung at midden sites close to the water's edge and along well-utilised hippo paths (Fig. 3L; Olivier & Laurie, 1974b). Thus, middens probably mark



Fig. 3. Photographic template of key hippo ecosystem engineering features from a variety of different locations. (A) Hippos congregate in tight-knit family groups (Tembe Elephant Park, South Africa; Wayne Matthews). (B) Hippos create grazing lawns (Chobe National Park, Botswana; Ekaterina Tsvetkova). (C) ‘Hippo lawn’ in an African forested ecosystem (Odzala National Park, Republic of Congo; Evan Hockridge). (D) Hippos eat and disperse sausage tree fruits (Luangwa River, Zambia; Jet Eliot). (E) Hippo pathway leading to and from water (Kruger National Park, South Africa; Michael Voysey). (F) Hippo paths can become large, scoured pathways (arrows indicate the presence of an erosion gully) (Kruger National Park, South Africa; Michael Voysey). (G) Hippos open up aquatic vegetation, creating new channels that link aquatic habitats (Kosi Bay Estuary, South Africa; Michael Voysey). (H) Pathways made by hippos become a network of river and swampland channels, maintaining water flow and connectivity for other aquatic life (Tembe Elephant Park, South Africa; Wayne Matthews). (I) Hippo paths leading from water to grazing grounds (Tembe Elephant Park, South Africa; Wayne Matthews). (J) Hippo channelling leading to increased river sinuosity and river heterogeneity (hippos in the image are encircled) (Kruger National Park, South Africa; Peter Boucher). (K) Hippos defecate large quantities of dung daily into aquatic ecosystems (Chobe River, Botswana; Claude Huot). (L) Hippos



Fig. 3 (Continued)

create ‘middens’ (i.e. nutrient hotspots) near water and along hippo paths (Kruger National Park, South Africa; Michael Voysey). (M) Large concentrations of hippo can lead to nutrient overload and water eutrophication (signs of eutrophication are indicated by arrowed green circles) (Tembe Elephant Park, South Africa; Wayne Matthews). (N) Fish eat hippo dung as well as ectoparasites occurring on hippos themselves (Mzima Springs, Tsavo East, Kenya; Mark Deeble/Vicky Stone). (O) Birds congregate near hippos to hunt fish attracted by hippo dung and invertebrates disturbed by hippo as they move through water (Mana Pools National Park, Zimbabwe; Henk Bogaard). (P) Increasing human–hippo conflict threatens the ecosystem engineering roles of hippos in some regions (Guinea-Bissau, Tete Sambu; from González *et al.*, 2016).

the periphery of a male hippo's territory (Estes, 2012), although hippo territoriality is poorly understood (Olivier & Laurie, 1974b). Other passing hippos sometimes add excrement to middens, suggesting that middens could also aid in communication and nocturnal navigation (Olivier & Laurie, 1974b). The manner in which hippos deposit dung and urine underpins how organic matter and key nutrients are transported across the landscape by hippos, and transferred between terrestrial and aquatic ecosystems.

Hippo family groups consist of a mature bull (upwards of 20 years old), and adult and sub-adult cows along with their offspring – a polygynous breeding system known as a harem whereby a single male defends access to multiple females (Smuts & Whyte, 1981). Hippo pod size is typically 10–15, but can range from 2–50 and even up to 150 animals during times of water scarcity (Estes, 2012; Inman *et al.*, 2022). Lower ranking bulls tend to occupy smaller, seemingly less satisfactory pools, and are more likely than mature bulls and females to occupy faster flowing river sections (Smuts & Whyte, 1981). Mature bulls aggressively defend access to females in the best water-based habitats, typically a 50–500 m stretch of shoreline, but are not considered territorial on land (Olivier & Laurie, 1974b). This social structure produces tightly associated family groups (Fig. 3A), resulting in highly concentrated aquatic ecological impacts. Furthermore, hippos are long-lived (life expectancy 35–50 years) and some individuals have been known to hold the same territories for up to 8 years in lakes and 4 years in rivers (Estes, 2012), resulting in long-lasting impacts.

Hippos inhabit a wide variety of aquatic environments, including major rivers, smaller non-perennial rivers, seasonal pans, natural lakes, wetlands, estuaries and human-made dams and weirs (Lewison & Pluháček, 2017). Unlike most other water-dependent herbivores (excluding dugongs *Dugong dugon* and manatees *Trichechus* spp.), hippos reside in the water itself, where they spend most daylight hours (Eltringham, 1999). Water is crucial to hippos for thermoregulation as they immerse their massive bodies and particularly sensitive skin (a thin epidermis with sweat glands that secrete a red, protective fluid; Saikawa *et al.*, 2004) in water to keep them cool and moist (Noirard *et al.*, 2008; Estes, 2012). To escape daytime heat, hippos typically only venture away from water at dusk, and spend the night time grazing (Smuts & Whyte, 1981). During drought, hippos may extend their grazing further away from water and into the daytime to obtain sufficient forage (Smit *et al.*, 2020). Similarly, on cool days, hippos often spend more time out of water due to the lower risk of dehydration, and are frequently observed basking on sandbanks. When in water, hippos prefer shallow areas with depths between 0.5 and 1.5 m (Chansa, Milanzi & Schone, 2011; Prinsloo, Pillay & O'Riain, 2020), gently shelving beaches (Field, 1970) and slow water velocity, which enable family groups to lie half-immersed, and where mothers can easily suckle their young (Olivier & Laurie, 1974b). Hippos are thus restricted to areas where there is water – confining, but also intensifying, their ecosystem engineering impacts.

The highest hippo population densities are known from the Luangwa River, Zambia, where up to 42 individuals per km of river have been documented (Tembo, 1987; Chomba *et al.*, 2013). High to moderate hippo densities have also been observed along the Great Ruaha River (26 animals km⁻¹; Stears *et al.*, 2018), Mara River (27 animals km⁻¹; Kanga *et al.*, 2011), Lake Edward (19 animals km⁻¹ shoreline; Lock, 1972), and in Kruger National Park along the Sabie (18 animals km⁻¹), Olifants (14 animals km⁻¹), and Letaba rivers (13 animals km⁻¹) (Smit *et al.*, 2020). These potential high densities, combined with their daily commute between water and grazing grounds, often using the same pathways (Fig. 3E; Lock, 1972), suggest that hippos can have profound influences on the geomorphology of both terrestrial and aquatic environments. Such effects include the mechanical actions of their partially webbed feet, which are small relative to their body size (Eltringham, 1999). These impacts compound over decades and centuries, especially where hippos occur at high densities.

III. HIPPO INFLUENCES ON TERRESTRIAL AND AQUATIC ENVIRONMENTS

Evidence suggests that behavioural and morphological traits of hippos, including their semi-aquatic lifestyle, make them an ideal candidate for extensive ecosystem engineering impacts. A unique facet of hippo ecology compared with other megaherbivores is their tendency to consume large quantities of vegetation from restricted parts of the terrestrial landscape, and then return to water where they defecate, thereby enriching aquatic environments with nutrients from terrestrial ecosystems, and impacting a host of ecosystem processes on land and in water (Fig. 4).

(1) The role of hippos in grazing lawn ecology

Hippos are grazers, foraging predominantly on C₄ grasses in savannas. Their high muzzle-width to body size ratio and muscular sharp-edged lips (Lock, 1972), make them highly suited to grazing lawn establishment by cropping grass just above the soil (Fig. 3B,C; Hempson *et al.*, 2015). Grazing lawns, or 'hippo lawns' when established by hippos (Olivier & Laurie, 1974b; Verweij *et al.*, 2006), are a distinct grassland community type characterised by short-statured grass species highly tolerant of grazing due to unique morphological adaptations, such as stolons and rhizomes, that keep important plant parts out of reach of grazers (Hempson *et al.*, 2015). These lawn grasses allocate more resources to nutrient-rich leaves than carbon-dense stems, and thus produce more grass leaf material per bite than tall erect-growing grass species. Accordingly, grazing lawns are highly productive and support large grazer populations, but require constant and repeated grazing for their maintenance. Although smaller herbivore species can maintain these short-grass patches, large-bodied short-grass specialists are often

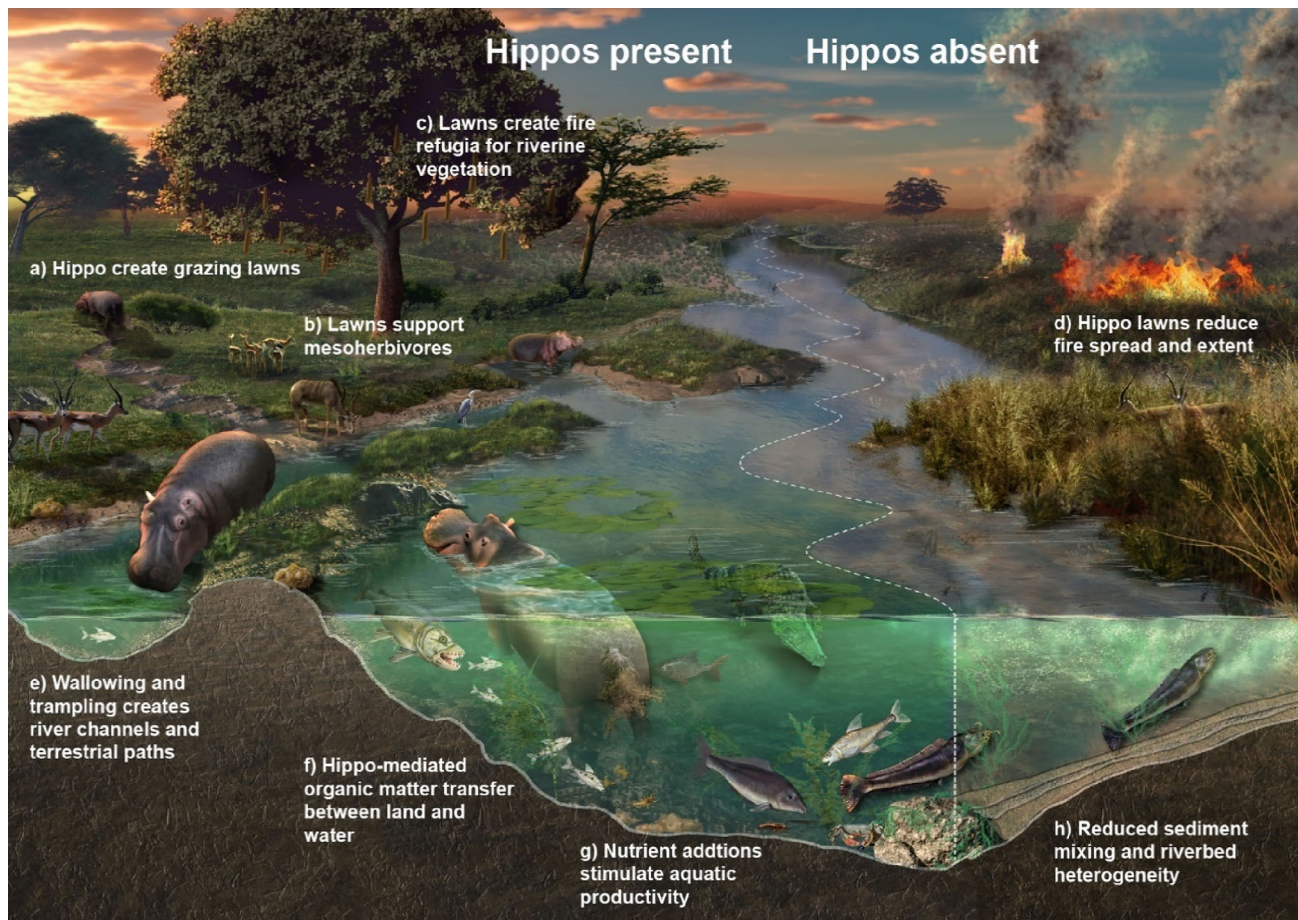


Fig. 4. Hippos play important ecosystem engineering roles in both terrestrial (a–e) and aquatic (e–h) environments. The absence of hippos from environments where they once occurred is likely to result in diminished ecological function. Figure prepared in collaboration with Nicolle Fuller/SayStudio.

vital for their establishment (e.g. hippo, white rhino, and to a lesser extent wildebeest *Connochaetes taurinus*) because these species are capable of consuming sufficient grass of low quality to initiate a switch in grass species composition (Hempson *et al.*, 2015). Grazing lawns created specifically by hippos have been found to be important for the subsistence of smaller mammalian herbivores, e.g. kob *Kobus kob* (Verweij *et al.*, 2006), impala *Aepyceros melampus* (O'Connor & Campbell, 1986), and warthog *Phacochoerus africanus* (Lock, 1972), and a variety of other taxa, including birds and invertebrates (Olivier & Laurie, 1974a; Eltringham, 1999).

Hippo grazing, and the extent of hippo-derived grazing lawns, is constrained by distance to water (Kanga *et al.*, 2011), but to what extent is less well known. In Queen Elizabeth National Park, Uganda, Lock (1972) observed that hippo grazing impacts, and the presence of lawn grass species, decline approximately 3.2 km from water. Other studies suggest that the maximum distance of hippo lawns from water is much shorter, e.g. 1.25 km (Olivier & Laurie, 1974b). Similarly, the prevalence of 'hippo lawns' in different environments is not well understood. Hippo lawn prevalence likely depends on the relative abundance of

hippos in an area, but other factors, such as terrain and forage availability, are also likely to play a deterministic role. Understanding spatial variation in hippo impacts is likely to be key for understanding their unique role as ecosystem engineers in much the same way that comprehending spatial variation in elephant impacts has been critical for the understanding and management of spatial heterogeneity (Owen-Smith *et al.*, 2006; Smit & Ferreira, 2010).

Hippo importance for grazing lawn establishment is predicted to be heightened in high-rainfall regions, where grass biomass is high, because only very large herbivores can consume enough grass biomass to keep grass short (Hempson *et al.*, 2015). Here, the hippo's enormous body size enables it to consume large quantities of forage, opening up tall-grass areas and initiating grazing lawns in areas that would otherwise be too dense and risky for smaller grazers more susceptible to predation (Sinclair, Mduma & Brashares, 2003; Radloff & du Toit, 2004; Owen-Smith & Mills, 2008; Le Roux *et al.*, 2018). However, where rainfall and productivity are high, hippos also move shorter distances because forage is easily accessible (Olivier & Laurie, 1974b; O'Connor & Campbell, 1986), potentially resulting in

grazing lawns being restricted to areas close to water (Fig. 3C). In more arid environments, grazing lawns are likely to be less spatially constrained by water, and establishment and maintenance by smaller herbivores could be more influential because of lower grass productivity and biomass (Verweij *et al.*, 2006).

Hippopotamuses are often assumed to facilitate grazing lawn establishment and maintenance. However, the pulling action of hippo grazing can also uproot grasses (Lock, 1972). Such uprooting could be counterproductive to grazing lawn establishment and potentially lead to grassland degradation, such as terrace erosion documented on the banks of the Mara River (Olivier & Laurie, 1974b). Hippo foraging behaviour – grazing on land but a large portion of egestion in water (McCauley *et al.*, 2015) – could also deprive grazing lawns of key nutrients. Smaller grazers typically return nutrients to lawns after foraging, *via* dung and urine deposition, which increases soil and foliar nutrients and further attracts grazers, maintaining lawns (Hempson *et al.*, 2015). However, hippos may destabilise this positive feedback loop (Lock, 1972; Owen-Smith, 1988; Stock, Bond & van der Vijver, 2010), in similar ways that white rhino and elephant do, as a result of the insensitivity of these species to predators relative to smaller-bodied herbivores, leading to less incentive to remain in high-visibility ‘predator-safe’ areas and thus to the return of digested material elsewhere in the landscape (Le Roux *et al.*, 2018). Consequences of nutrient export away from lawns by hippos remain largely unknown, but are potentially inconsequential if these hippo lawns are established in already nutrient-rich river floodplains.

(2) Direct and indirect impacts of hippos on woody plant demographics

Traditionally considered obligate grazers, consuming mostly C₄ grasses, growing evidence indicates that hippos incorporate more herbaceous (forbs) and woody C₃ plants in their diet than previously assumed (Cerling *et al.*, 2008; Chritz *et al.*, 2016). The dietary fraction of C₃ biomass consumed by hippos relative to other grazers appears to lie between species typically considered pure grazers (e.g. zebra *Equus quagga*, buffalo *Syncerus caffer*, warthog *Phacochoerus africanus*), which consume hardly any C₃ material, and mixed feeders such as impala (Cerling *et al.*, 2008). Increased proportions of C₃ plants (i.e. forbs and woody plants) in hippos diets tends to coincide with periods or sites of low grass availability, such as where woody plants have expanded into the grass layer due to woody encroachment, or during drought (Chritz *et al.*, 2016). Implications of such dietary flexibility for savanna grasslands remain to be thoroughly explored, but preliminary evidence suggests that hippos may play a role in regulating woody plant structure at young demographic stages, namely seedlings and small saplings. For instance, McCauley *et al.* (2018) demonstrated that while hippos did not significantly impact woody plant abundance in control compared to exclosure plots over a three-year period, hippo presence significantly reduced woody plant height. It

could be that hippos only consume woody seedlings and saplings as a by-product while grazing because their broad muzzle permits a relatively low degree of selectivity (Eltringham, 1999). Nevertheless, this foraging behaviour results in heavily grazed, short-grass areas remaining largely devoid of woody plants, perhaps even in the absence of browsers (Voysey *et al.*, 2020).

Arguably the most important impact of hippos in shaping woody plant demographics may come about indirectly, *via* their impact on fire regimes, particularly fire spread. In addition to herbivory, fire is a major limiting factor for woody plant survival and recruitment in savannas, causing high seedling and sapling mortality, and preventing young trees from growing tall and producing seeds (Case & Staver, 2016; Gignoux *et al.*, 2009; Higgins *et al.*, 2007). Heavily grazed, short-grass areas established by hippos can act as fire breaks, leading to fire suppression. Along the Mara River, for instance, short grass patches created by hippos were interspersed with a matrix of high-density acacia thorn trees (*Acacia kockii*, *A. gerardii*, and *A. drepanolobium*) growing amongst tall grass swards that had escaped seasonal fires because of hippo-induced patchiness in grass biomass (Olivier & Laurie, 1974b). Where hippos create such patchiness, there is insufficient fuel available for fires to spread, creating a patch mosaic of burnt and unburnt areas and promoting landscape-scale heterogeneity in tree survival and recruitment. Since hippos are constrained to water (Kanga *et al.*, 2013; Stears *et al.*, 2019), fire suppression from hippo grazing is likely to be particularly important for maintaining densely wooded areas along rivers (Olivier & Laurie, 1974b; Smit & Archibald, 2019), and could be important for the ecological diversity and persistence of fire-sensitive riparian vegetation and woody species, e.g. sycamore fig (*Ficus sycomorus*). Hippos could further aid riparian vegetation by facilitating seed dispersal for select tree species. Hippos are known to consume the fruit of riparian sausage trees (Fig. 4D), with sausage tree fruits found in a high proportion of hippo stomachs (Ansell, 1965), suggesting a potentially important role of hippos in their seed dispersal (Namah *et al.*, 2019).

(3) Hippo influences on geomorphology, both on land and in water

Hippo trail formation represents an important geomorphological process (Fig. 3E; McCarthy *et al.*, 1998a; Deocampo, 2002; Mosepele *et al.*, 2009). Over time, hippo trails become free of vegetation, resulting in the development of scoured pathways that can be up to 5 m wide and 1 m deep (Fig. 3F; McCarthy *et al.*, 1998a; Deocampo, 2002), which can lead to the development of new river channels (Fig. 3G, H). Similarly, hippo trails can become a source of wetland expansion, breaking through embankments, and opening up water flow into new areas and away from others (Fig. 3G,H; McCarthy *et al.*, 1998a). Moreover, hippos prevent existing river channels from becoming clogged by sediments and aquatic vegetation when wading through water

(Fig. 3H–J), even though they do not eat aquatic plants (Naiman & Rogers, 1997). The best documented impacts of hippos on fluvial geomorphology originate from the Okavango Delta, Botswana, where hippos are key determinants of wetland responses to changing seasonal conditions and may be more important than any other megafauna species in shaping this vast wetland ecosystem (McCarthy *et al.*, 1998a). The Nqoga Channel, for example, is thought to have originated directly from hippo activity (Tinley, 1966; McCarthy *et al.*, 1998a). Conversely, declines in hippo populations elsewhere, due to exploitation and hunting, may have led to channel closure (Stigand, 1923; McCarthy & Ellery, 1995).

Although hippos are widely considered pivotal in determining fluvial characteristics of wetlands (e.g. McCarthy *et al.*, 1998a; Mosepele *et al.*, 2009), little empirical support is available. A more comprehensive understanding of their impact in comparison with other important hydrological determinants is required. Aspects such as seasonality of water flow, substrate type, and the actions of other ecosystem engineers, such as island formation by termite mounds (McCarthy, Ellery & Dangerfield, 1998b) and elephants, which also regularly venture into water (Mosepele *et al.*, 2009), warrant consideration. Likewise, in other important aquatic habitats for hippos (e.g. rivers, seasonal pans), very little research has been conducted to establish the abundance and frequency of hippo-derived geomorphological features, despite anecdotal evidence suggesting they are widespread and common.

(4) Biogeochemical cycling by hippos in rivers and other waterways

Animals that move between ecosystems can strongly influence the transboundary flow of material and nutrients (Polis, Anderson & Holt, 1997; Vanni, 2002; Ellis-Soto *et al.*, 2021). For both the donor and recipient ecosystem, resource flow can have a significant impact on ecological function, such as nutrient cycling (Vanni, 2002), primary productivity (Marcarelli *et al.*, 2011) and food-web dynamics (Leroux & Loreau, 2008). Hippo-mediated organic matter flow from terrestrial to aquatic ecosystems is a prime example of an animal-mediated resource subsidy, whereby large quantities of organic matter are transferred daily from one ecosystem to another. Given that a single adult hippo consumes ~40–50 kg of organic matter (wet mass) during a single nocturnal foraging excursion on land (Lewison & Carter, 2004; Pennisi, 2014), with a large proportion of this forage intake later egested in water *via* dung and urine (Fig. 3K), hippo nutrient subsidies into aquatic environments can be substantial. Recent estimates of hippo organic matter loading into the Mara River suggest that a resident hippo population of ~4000 individuals egest ~36,200 kg faeces day⁻¹ into the river (Subalusky *et al.*, 2015). The proportion of material egested into water likely depends on how much time hippos spend in water, which is thought to vary throughout the year (Subalusky *et al.*, 2015; Schoelynck *et al.*, 2019).

Daily loading of organic matter and nutrients by hippos into waterways plays a critical and complex, although still relatively understudied, role in biogeochemical cycling. Recent studies suggest that the availability of key nutrients and chemical constituents in aquatic environments is altered by hippos (Subalusky *et al.*, 2015, 2018; Stears *et al.*, 2018; Dawson *et al.*, 2020; Dutton *et al.*, 2020), including limiting nutrients for plants such as N and P (Masese *et al.*, 2020), which can alter ecosystem functioning by promoting plant and algal growth when deposited in sufficient quantities (Subalusky *et al.*, 2015; McCauley *et al.*, 2018). In terrestrial settings, hippo grazing does not appear to increase the concentrations of plant limiting nutrients (e.g. N and P) as these are probably deposited in water instead (McCauley *et al.*, 2018; Subalusky *et al.*, 2018; Masese *et al.*, 2020). Thus, hippo-vectored nutrient inputs are thought to invigorate aquatic life more strongly, increasing the diversity of aquatic communities (Mosepele *et al.*, 2009). Even expanding non-native hippo populations in Columbia (Subalusky *et al.*, 2021; Castelblanco-Martinez *et al.*, 2021) have been shown to stimulate aquatic ecosystem metabolism (Shurin *et al.*, 2020).

The cycling of Si is another important biogeochemical process impacted by hippos (Schoelynck *et al.*, 2019). The unique role of hippos in the Si cycle lies in their ability to process grass material containing Si and egest it directly into water, circumventing the slower process of Si entering water *via* soil additions. Consequently, hippos contribute up to 76% of the total Si flux in the Mara River (Schoelynck *et al.*, 2019). The ecological significance of this hippo-induced surge in Si availability is still being investigated, but it is thought to increase the primary productivity of diatom-dominated phytoplankton communities that could otherwise be suppressed if hippos were absent (Schoelynck *et al.*, 2019). Yet, the extent to which overall river ecosystem health depends on direct Si inputs from hippos remains unexplored.

At some sites and during drier periods excessive organic matter loading and nutrient input by hippos can result in nutrient overload in aquatic environments (Fig. 3M; Dutton *et al.*, 2020), leading to hypoxia and large-scale die-offs of fish communities (Dutton *et al.*, 2018b), and the alteration of food-web dynamics towards higher bacterial contributions (Dawson *et al.*, 2020). High water discharge (e.g. during the wet season) facilitates flushing of hippo-derived organic matter downstream, enabling nutrients to disperse widely. By contrast, stagnant water with low discharge (e.g. in the dry season) leads to organic matter and sediment build-up in more isolated river sections and pools, which can lead to water eutrophication, lower dissolved oxygen levels, and increased water turbidity and sediment loads (Wolanski & Gereta, 1999; Dutton *et al.*, 2018a; Stears *et al.*, 2018). Such conditions can be further exacerbated during dry periods when hippos aggregate in large numbers where water persists (Stommel, Hofer & East, 2016; Fritsch *et al.*, 2022), which can also have direct impacts on species co-occurring with hippos. For instance, during the dry season, high-density hippo pools have lower dissolved oxygen than pools with low hippo density, compelling fish to position themselves higher up in

the water column where sufficient oxygen is available. High-density hippo pools consequently attract more fish-eating birds because their prey is closer to the water surface and therefore easier to catch (Stears & McCauley, 2018). River characteristics and flow regimes, seasonal context and the interplay between water availability and hippo density can therefore significantly alter hippo effects on biogeochemical cycling (Mosepele *et al.*, 2009; Stears *et al.*, 2018; Dutton *et al.*, 2020), which, in turn, can affect a diverse array of other species (Stears & McCauley, 2018; Dawson *et al.*, 2020).

Developing an understanding of how hippo ecological impacts may vary in response to changing river flow regimes is becoming increasingly critical. As African savannas become hotter and more arid (Arnell & Gosling, 2013; Nicholson, 2017), hippos may be forced into smaller and more isolated aquatic habitats (Fritsch *et al.*, 2022), increasing the likelihood of subsidy overload to the detriment of aquatic biodiversity (Dawson *et al.*, 2016; Dutton *et al.*, 2018b; Masese *et al.*, 2018). In future, and already in some areas (Smit *et al.*, 2020), such a dilemma could become analogous to the problem of growing elephant numbers in small, fenced reserves, whereby high elephant abundance leads to unintended vegetation responses and declines in biodiversity (Kerley & Landman, 2006; Guldmond *et al.*, 2017). Nonetheless, high hippo numbers historically may have also led to considerable ecological change, and therefore we have no ecological reference state for hippo ecosystem engineering in African waterways (Moss, 2015). Thus, it would be prudent for scientists and managers alike to continue to develop our understanding of how changing river flow regimes might alter the ecological roles of hippos.

IV. COMPARISON OF HIPPOS WITH OTHER AFRICAN MEGAHERBIVORES

Hippos appear to influence a greater diversity of ecosystem components than any other African megaherbivore (Table 1), primarily because of their impacts in both terrestrial and aquatic environments. No other megaherbivore has such notable impacts across more than one ecosystem type, even though other megaherbivores may also occasionally venture into water to gain access to adjoining terrestrial habitats or to cool down and wallow (Naiman & Rogers, 1997; Mosepele *et al.*, 2009; Croomsigt & Te Beest, 2014). In rivers, wetlands and other major waterways, hippos shape not only the physical ground *via* trampling, but also the biogeochemistry of the entire aquatic environment (Subalusky *et al.*, 2015; Stears *et al.*, 2018; Dutton *et al.*, 2020). In essence, hippos regulate and modify the entire living medium of water, which other aquatic and semi-aquatic species are dependent on (ranging from diatoms to fish, birds and crocodiles), some of which require relatively specialised conditions that hippos have the potential to modify (Dutton *et al.*, 2018a,b). Terrestrial megaherbivores, in comparison, are less capable of altering the medium in which

other animals exist, i.e. the atmosphere, even though toppling of trees by elephants can regulate aboveground carbon storage (Berzaghi *et al.*, 2019; Davies & Asner, 2019), and fermentation of plant material inside large herbivore stomachs can contribute to global methane emissions (Smith *et al.*, 2016). Even when considering only their terrestrial influence, hippos have a diverse array of impacts that are comparable to those of other terrestrial megaherbivores (Table 1).

On land, the ecological role of hippos is most comparable to that of the white rhino, a similar sized megagrazer. While white rhinos also reduce grass biomass, create grazing lawns and promote patchiness in fire regimes (Waldram, Bond & Stock, 2008; Croomsigt & Te Beest, 2014), they are less constrained by proximity to water than hippos. It is unclear how characteristics, such as species composition and spatial distribution, of grazing lawns created by these two megagrazers compare, although structurally they are expected to be similar. In light of widespread population declines of white rhino due to rampant poaching (Ferreira *et al.*, 2017, 2018), it is pertinent to consider whether these two megagrazers are capable of complementing each other functionally. Specifically, we need to determine the capacity to which hippos are capable of replacing the functional roles of white rhino should these be extirpated either locally or outright.

Elephants also consume large quantities of grass material, particularly during the wet season when grass is most abundant and nutritious (Codron *et al.*, 2006). However, elephants do not crop grass short like hippos and white rhinos, but rather pluck clumps of tall grass from the soil using their trunk; their grazing is therefore not thought to lead to grazing lawn formation or shape fire regimes. However, elephants exert strong influences on woody vegetation (Guldmond *et al.*, 2017) through consumption, tree felling (Asner & Levick, 2012), and seed dispersal (Dudley, 2000; Cochrane, 2003; Bunney *et al.*, 2017). These impacts on woody vegetation can lead to large-scale ecosystem effects on nutrient cycling (Skarpe *et al.*, 2004; Parker, Bernard & Adendorff, 2009), fire regimes (Kimuyu *et al.*, 2014), carbon storage (Davies & Asner, 2019; Berzaghi *et al.*, 2019) and habitat availability for other species (Table 1; Kerley & Landman, 2006; Guldmond *et al.*, 2017). Hippos have comparatively fewer direct impacts on woody vegetation (McCauley *et al.*, 2018), but their indirect impacts on woody plants *via* modification of fire spread and extent could have more substantive effects on woody vegetation than currently realised. Thus, hippos could have similar, although more cryptic and indirect, impacts on woody vegetation as elephants.

Megabrowsers, i.e. giraffes and black rhinos, have seemingly little overlap with hippos from a dietary or ecosystem engineering perspective. However, black rhinos have been shown to browse more frequently on grazing lawns than tall-grass areas because the small size classes of acacia trees they prefer are more visible and detectable when grass is short (Emsley & Adcock, 1994; Bond, Smythe & Balfour, 2001). Since hippos also reduce the height of woody

Table 1. The ecological engineering influence of hippos and other extant African megaherbivores on various ecosystem components. Hippos influence a greater number of ecosystem components than any other African megaherbivore, largely due to their additional engineering role in aquatic ecosystems. Column headings adapted from Hyvärinen *et al.* (2021).

Megaherbivore species	Vegetation structure	Terrestrial biodiversity	Fire	Seed dispersal	Biogeochemistry	River hydrology and geomorphology	Aquatic biodiversity
Common hippopotamus (<i>Hippopotamus amphibius</i>) Adult body mass: 1365–2600 kg Population: 115,000–130,000	Transform tall grassland into grazing lawns, especially near water. ¹ Consume woody seedlings that help keep ‘hippo lawns’ open. ²	Nutritious forage on lawns attracts small herbivore species, and lawn openness provides safety from predators. ¹	Hippo lawns act as natural fire breaks, altering local fire regimes along water courses, ³ protecting fire-sensitive woody species along rivers.	Potentially an important disperser of <i>Kigelia africana</i> (sausage tree) ⁴ and other riverine woody species (e.g. <i>Faidherbia albida</i>). ⁵	Transport large quantities of organic matter and nutrients away from terrestrial feeding grounds into aquatic habitats (e.g. rivers and dams), ⁶ including dissolved oxygen levels and water turbidity. ⁹	Maintain and deepen river channels and scour out new ones. ^{7,8} Extensive impact on water chemistry, including dissolved oxygen levels and water turbidity. ⁹	Cascading effects on primary productivity and aquatic biodiversity (e.g. invertebrates, fish) through biogeochemistry and hydrology impacts. ^{9,10}
African savanna and forest elephant (<i>Loxodonta africana</i> and <i>L. cyclotis</i>) Adult body mass: 2500–6000 kg Population: 415,000	Topple and damage large trees, reduce woody cover and increase woody debris. ¹¹	Woody cover changes have cascading effects on biodiversity, including insects, reptiles, birds, rodents and ungulates. ^{11,12}	Consume large quantities of grass biomass, reducing fuel available for fires and fire temperature. ¹³	Important disperser of many African tree species. ^{14,15} Ingestion of seeds helps prevent insect infestation, and improves germination success. ¹⁶	Tree topping stimulates nutrient cycling, ^{17,18} and reduces aboveground carbon in savannas. ¹⁹ Conversely, forest elephants increase aboveground carbon in African rainforests. ²⁰	Might assist with channel opening and maintenance in certain areas	No known effects
White rhinoceros (<i>Ceratotherium simum</i>) Adult body mass: 1600–23,00 kg Population: 17,212–18,915	Transform tall grassland into grazing lawns. Less constrained by water than hippos. ²¹	Nutritious lawns attract smaller herbivore species, and provide safety from predators. ²¹ Short grass areas attract unique bird communities. ²²	Create grazing lawns that act as natural fire breaks, altering local fire regimes. ²¹	Might assist in the dispersal of grass seeds.	Export nutrients away from nutrient-rich grazing lawns due to less fear of predation than smaller herbivores. ²³ Create nutrient-rich dung middens. ²¹	No known effects	No known effects
Black rhinoceros (<i>Diceros bicornis</i>) Adult body mass: 700–13,00 kg Population: 5630	Open up high-density wooded areas, and change woody structure towards	No known effects	Might improve fire permeability into otherwise densely wooded areas. ²⁴	Consume and disperse the seeds of a number of <i>Acacia</i> tree species, and	Create nutrient-rich dung middens. ²⁶	No known effects	No known effects

(Continues on next page)

Table 1. (Cont.)

Megaherbivore species	Vegetation structure	Terrestrial biodiversity	Fire	Seed dispersal	Biogeochemistry	River hydrology and geomorphology	Aquatic biodiversity
Giraffe (all species) (<i>Giraffa giraffa</i> , <i>G. reticulata</i> , <i>G. camelo</i> <i>pardalis</i> , and <i>G. tippelskirchi</i>) Adult body mass: 800– 1200 kg Population: 117,000	smaller size classes. ²⁴ Prune the tops of trees, changing tree architecture, and reducing overall tree height, further suppressing seed produ- ction. ^{25,27}	Extensive browsing alters woody species composition and distribution. ²⁷	No known effects	possibly others. ²⁵ Consume and disperse the seeds of a number of <i>Acacia</i> tree species. ^{25,28}	No known effects	No known effects	No known effects

1, Verweij *et al.* (2006); 2, McCauley *et al.* (2018); 3, Olivier & Laurie (1974b); 4, Namah *et al.* (2019); 5, Dunham (1990); 6, Subalusky *et al.* (1998a); 8, Mosepele *et al.* (2009); 9, Sears *et al.* (2018); 10, Stears & McCauley (2018); 11, Gulderson *et al.* (2017); 12, Kerley & Landman (2006); 13, Kimuyu *et al.* (2014); 14, Bunney *et al.* (2017); 15, Dudley (2000); 16, Cochrane (2003); 17, Skarpe *et al.* (2004); 18, Parker *et al.* (2009); 19, Davies & Asner (2019); 20, Berzaghi *et al.* (2019); 21, Waldram *et al.* (2008); 22, Krook *et al.* (2007); 23, Le Roux *et al.* (2018); 24, Luske *et al.* (2009); 25, Coe & Coe (1987); 26, Taitman *et al.* (2000); 27, Bond & Loffell (2001); 28, Miller (1996).

seedlings and saplings on grazing lawns (McCauley *et al.*, 2018), both black rhinos and hippos could be important for maintaining open lawns. Hippos and megabrowsers could also overlap in their role as seed dispersers (Miller, 1996). Hippos eat the fruits and seed pods of certain riparian trees, which they probably also disperse and help germinate (Dunham, 1990; Namah *et al.*, 2019), and giraffes, black rhinos and elephants disperse seeds from a wide variety of savanna and forest tree species [e.g. *Tieghemella heckelii* (Feer, 1995); *Acacia erioloba*, *Schlerocarya birrea* (Dudley, 2000); *Balanites wilsoniana* (Cochrane, 2003)]. However, hippos appear to consume and disperse seeds from different tree species than these megabrowsers, perhaps leading to complementary rather than overlapping contributions to ecosystem-level seed dispersal.

As megaherbivores pass through the landscape, they attract a diverse array of organisms. For instance, some birds (e.g. red and yellow-billed oxpeckers; *Buphagus erythrorhynchus* and *B. africanus*, respectively) eat a variety of ticks (Ixodoidea) directly off their large-herbivore hosts, including from hippos (Dean & MacDonald, 1981; Petney & Kok, 1993; Weeks, 2000). Large herbivores also flush invertebrates (e.g. grasshoppers and butterflies), assisting the foraging of insect-eating birds (e.g. cattle egrets *Bubulcus ibis* and fork-tailed drongos *Dicrurus adsimilis*) (Dean & MacDonald, 1981; Kioko *et al.*, 2016; Mikula *et al.*, 2018). In water, hippos fulfil a similar function. Certain fish species, such as mudfish *Labeobarbus* and *Barbus* spp., African catfish *Clarias gariepinus*, and Mozambique tilapia *Oreochromis mossambicus* have been observed foraging on hippo dung and aquatic invertebrates disturbed by hippos in water (McCauley *et al.*, 2015; Dawson *et al.*, 2020). Mudfish have also been observed feeding directly off hippos, probably on ectoparasites and dead flesh near wounds (Fig. 3N). These findings support anecdotes of fishermen improving their catch success when fishing near hippos (Eltringham, 1999; Mosepele *et al.*, 2009). Similarly, fish-eating birds (e.g. grey heron *Ardea cinerea*, pied kingfisher *Ceryle rudis*, and various cormorant species) display feeding associations with hippos, sometimes perching and hunting directly from their backs (Fig. 3O; Eltringham, 1999). Above water, but still in aquatic habitats, African jacana *Actophilornis africanus*, exhibit a feeding association with hippos by eating ectoparasites off their skin and insects that they flush (Ruggiero, 1996), in much the same way that non-wading birds feed alongside terrestrial megaherbivores (Dean & MacDonald, 1981).

Despite their large body size, hippos contrast with other megaherbivores by being central place foragers, returning to roughly the same place after each foraging excursion (Eltringham, 1999; Lewison & Carter, 2004). Moreover, hippos spend approximately 12–18 h per day in water (Subalusky *et al.*, 2015). Consequently, hippos do not roam or forage over as spatially expansive areas as other megaherbivores, but likely utilise the landscape more intensively in areas that they do occupy, resulting in more concentrated and localised engineering impacts. However, all megaherbivores, including hippos, are less susceptible to

predators than are smaller herbivores, and, as a result, the spatial distribution of their impacts is less influenced by predator-induced landscapes of fear (Le Roux *et al.*, 2018). Therefore, hippo grazing and associated impacts are less influenced by landscape features that provide safety from predators for smaller grazers (e.g. blue wildebeest *Connochaetes taurinus* selecting predator-safe hillcrests; Yoganand & Owen-Smith, 2014).

Lastly, compared to other large herbivores, hippos have approximately half the daily forage intake relative to body mass (Field, 1970; Schwarm *et al.*, 2006; Clauss *et al.*, 2007). Hippos are also the only megaherbivore (and largest living species on Earth) with a foregut fermentation anatomy (Field, 1973; Eltringham, 1999). Consequently, they have a higher gut retention time compared with other megaherbivores (e.g. elephants; Clauss *et al.*, 2007), and lower daily forage intake relative to body mass, which could result from a combination of their anatomy and much higher nutrient content of their diet. Hippos can therefore afford to spend less time foraging than other megaherbivores (Clauss *et al.*, 2003). Moreover, hippos semi-aquatic lifestyle results in lower thermal stress (Coughlin & Fish, 2009), which could contribute to their reduced energy expenditure and shorter foraging time compared with other megaherbivores (Wyatt & Eltringham, 1974; Owen-Smith, 1988). Nevertheless, because hippos are required to consume high-quality grass, they need to forage in very specific areas, further concentrating their impacts. Furthermore, the considerable time hippos spend in water and not grazing facilitates hippo-induced geomorphological change, which is not the case for other megaherbivores.

V. HIPPO CONSERVATION AND HUMAN INFLUENCES ON HIPPO ECOSYSTEM ENGINEERING

African rivers are typically seasonal, experiencing reduced water flow in the dry season. However, rampant water extraction to support growing agricultural demands and changing rainfall patterns due to human-induced climate change are disrupting natural flow regimes and flow rates, causing a decline in the ecological status of rivers globally (Nilsson *et al.*, 2005; McClain, 2013; McClain *et al.*, 2014). Hydrological changes to African watersheds have the potential to eliminate hippos entirely from certain regions, and are likely to intensify hippo effects on biogeochemical cycling. For example, nearly two decades of mouth closure in South Africa's St Lucia Estuary, driven by drought and upstream anthropogenic catchment modification, has caused excessive build-up of hippo organic matter on the estuary bed, which has led to declines in the abundance, biomass and richness of benthic macroinvertebrate communities and microphytobenthic biomass (Dawson *et al.*, 2016), as well as increased bacterial biomarker levels amongst resident fish populations (Dawson *et al.*, 2020).

Effective river management is crucial for the long-term persistence of viable hippo populations (Eksteen *et al.*,

2016). Agricultural expansion into river floodplains, and water extraction for crop irrigation threaten river health and hippo population persistence (Kanga *et al.*, 2012; Timbuka, 2012; Eksteen *et al.*, 2016; Stommel *et al.*, 2016). Expanding agriculture in the vicinity of rivers encourages river siltation, filling up hippo pools with sediment (Dutton *et al.*, 2018a), and increases water demand for crop irrigation, resulting in lower and more erratic water levels and increasing hippo encounter rates with people. Therefore, the primary conservation intervention for hippos should be responsible water flow and river quality management (Dutton *et al.*, 2020). Interventions should limit water extraction and eliminate pollutants and excessive nutrients that could exacerbate hippo impacts (Eksteen *et al.*, 2016).

Other conservation actions for hippos include buffer zones along rivers that exclude agriculture and human settlement, and providing adequate space for hippos to live alongside people and avoid frequent conflict (Stears *et al.*, 2019). Corridors between croplands could provide safe hippo passageway, and these approaches should be explored in areas where people and hippos coexist. Another pragmatic conservation measure that warrants consideration is the artificial supplementation of water bodies. Man-made dams and weirs have often provided the only lifeline for hippos under severe scenarios of river siltation, water extraction and pollution (Jacobsen & Kleynhans, 1993; Utete, 2020). Management initiatives that create hippo habitat are likely to increase the spatial extent of hippo grazing and connectedness between grazing grounds, which warrants consideration before implementation (Smit *et al.*, 2020).

Crucial to the persistence of hippo ecosystem engineering is an integrated understanding of hippos in social–ecological systems (Post, 2017). Hippos are unpredictable and dangerous, and are responsible for a greater loss of human life than any other large African animal other than crocodiles (Dunham *et al.*, 2010; Chomba *et al.*, 2012). Hippos are also notorious crop raiders (Fig. 3P; Clarke, 1953; Mkanda, 1994; Kendall, 2011; Massé, 2016; González *et al.*, 2016), and are well known for attacking local fishermen (Eltringham, 1999). Conversely, human exploitation of hippos and their habitat is responsible for their population decline in many areas (Lewison, 2007; Zisadza *et al.*, 2010; Kanga *et al.*, 2012; Scholte & Iyah, 2016; Utete, 2020). Hippos often venture outside protected areas because their aquatic habitats render fences less restrictive to their movements, making hippos more prone to encounters with people than many other large mammals (Mackie, Dunham & Ghiurghi, 2013; Post, 2017; Baker *et al.*, 2020). Furthermore, hippos venturing into human-inhabited landscapes, often referred to as ‘problem animals’, are routinely shot and killed (Mkanda, 1994; Chomba *et al.*, 2012; Utete, 2020) without much consideration for their vulnerable conservation status (Lewison & Pluháček, 2017). Therefore, ensuring human–hippo coexistence and maintaining the unique ecosystem engineering role of hippos requires a far more nuanced understanding of the complex interactions between hippos and people (van Houdt & Traill, 2022).

Effective hippo conservation should begin with a theoretical framework for managing human–hippo interactions in complex social–ecological systems, with consideration for the uniqueness of hippo behaviour (e.g. nocturnal and semi-aquatic lifestyle). Studies seeking to understand the severity of human–hippo conflict across different environments and human populations, as well as the effectiveness of solutions to prevent and reduce the impacts of human–hippo conflict are essential (Van Houdt & Traill, 2022). Notably, where they occur alongside people in relative harmony, hippos probably help support human livelihoods, for example, by bolstering nutrient inputs that stimulate aquatic food chains (Subalusky *et al.*, 2018), promoting robust fish populations (Mosepele *et al.*, 2009; McCauley *et al.*, 2015; Stears *et al.*, 2018), or attracting ecotourism. Thus, hippo conservation is not only important for maintaining the unique ecosystem engineering role of hippos, but also for supporting human livelihoods, as long as conflicts between people and hippos are addressed.

Hydrological changes and increased climatic variability are predicted to exacerbate disease outbreaks among wildlife (Dorner *et al.*, 2006; Collender *et al.*, 2016; Wang *et al.*, 2021). For hippos, their semi-aquatic life history, gregarious nature, and ability to engineer aquatic environments render them not only vulnerable to disease (Dutton *et al.*, 2021), but also potential vectors and creators of environments conducive to disease proliferation. An example is the transmission of anthrax, a zoonotic disease caused by the soil-dwelling bacteria *Bacillus anthracis* (Van Ness, 1971; Hampson *et al.*, 2011). Anthrax has a low potential for direct live animal-to-animal transmission, and infection is mainly through direct uptake of spores from the environment (Van Ness, 1971; Hampson *et al.*, 2011). However, occurrences of carnivory and cannibalism among hippos have been identified as an additional mode of anthrax transmission between individuals (Dudley *et al.*, 2016) with several documented anthrax outbreaks involving hippos (Driciru *et al.*, 2018; Stears *et al.*, 2021). In Uganda's Queen Elizabeth National Park, anthrax infections amongst hippos spread in a direction that matched the natural water flow as infected hippo carcasses were carried downstream, interspersing among live animals, and facilitating disease transmission (Driciru *et al.*, 2018). Stears *et al.* (2021) observed that hippo-induced anthrax transmissions moved in the opposite direction to natural water flow due to anthropogenic modifications of the Great Ruaha River's natural flow, causing extreme drying and prompting anthrax-infected hippos to walk upstream in search of aquatic refugia.

VI. FUTURE RESEARCH DIRECTIONS AND CHALLENGES

Unravelling the ecosystem engineering role of hippos is challenging because of their semi-aquatic lifestyle and nocturnal grazing behaviour, which makes direct observational studies difficult. Moreover, hippos are highly unpredictable and

notoriously dangerous to field researchers, particularly when out of water. To combat these challenges, alternative approaches to observing hippos have become increasingly useful. For instance, observations of captive animals have assisted in determining excretion and egestion rates of hippos (Schwarm *et al.*, 2006; Subalusky *et al.*, 2015), and drone imagery has become a viable method for counting hippos (Linchant *et al.*, 2018; Inman *et al.*, 2019; Fritsch & Downs, 2020). Nevertheless, many scientific challenges remain. Hippo population dynamics and many aspects of their social lives remain unknown despite group size and density likely being key for determining hippo engineering impacts (Sayer & Rakha, 1974; Inman *et al.*, 2022; Fritsch *et al.*, 2022). Understanding hippo population dynamics, and ecological impact, would benefit tremendously from the establishment of methods to assign individuals with unique identifiers (e.g. ear tags or natural marks), thus enabling individual life histories and populations to be tracked over time.

One research direction that would significantly improve our ability to decipher hippo ecological impacts, and assist with uncovering their behavioural and social dynamics, is the study of hippo movements. Animal movements underpin how key resources are utilised to survive and reproduce (Kays *et al.*, 2015) and can assist with understanding animal nutrient subsidies and transport (Ellis-Soto *et al.*, 2021). Hippo movement patterns remain an almost unexplored facet of their ecology (but see Stears *et al.*, 2019), especially when compared with other megaherbivores. In many respects, the night time habits of hippos remain completely undocumented. Ultimately, this lack of insight on where hippos go severely hampers our ability to understand their ecological impacts, as well as to conserve and manage them effectively, especially in human-dominated landscapes. A more nuanced perspective of hippo movements would facilitate much greater insight into their ecological role, and how this role might vary in different habitats. For example, hippo movement and ecological impact could differ with water body type as different aquatic habitats (e.g. rivers, dams, estuaries) vary in terms of the seasonal occupancy of hippos (Fritsch *et al.*, 2022). Hippo movement studies could also help demonstrate where in the landscape their impacts are most concentrated and at what distance away from water these effects dissipate. Movement studies could also elucidate whether the ecological effects of hippos overlap and interact spatially with those of other megaherbivores.

The challenges facing hippo movement studies are not trivial. First, hippos pose a real danger to handlers and veterinarians attempting to attach tracking devices. Second, hippos are highly sensitive to the opioid-containing drugs traditionally used for immobilisation, with approximately one in three hippos dying during tranquilisation (Peter Buss, personal communication). Third, only certain environments are conducive for hippo tranquilisation. If darting is attempted too close to water, hippos can retreat into water before they are darted. Alternatively, if a hippo is successfully darted but then retreats to water before the tranquiliser can

take effect, it can drown. However, recent advances in drug combinations used to immobilise hippos have helped to maintain their breathing response, lowering the risk of drowning and reducing death rates overall (Stalder *et al.*, 2012; Boothe *et al.*, 2016). Lastly, an effective device attachment method for hippos is still to be devised because their stout necks prevent the use of neck collars.

To date, the only published study on hippo movements made use of ankle collars—modified versions of collars used for tracking rhinos (Stears *et al.*, 2019; Pfannerstill *et al.*, 2022). Using this approach, Stears *et al.* (2019) successfully tracked the movements of 10 male hippos, for a maximum of 1 year per animal in the Great Ruaha River ecosystem. Males were selected because they were predicted to show greater responses to hydrological variability and because they are easier to isolate for darting. Hippo movement data from this study provide unique insights into the ecosystem engineering role of hippos. For example, Stears *et al.* (2019) demonstrated that male hippo movements are highly constrained to water, but that these movements vary considerably by age class and season. During the wet season, home range size of large sub-adult males was threefold greater than dominant and small sub-adult males. Large sub-adults expanded their home ranges (dry season 2.5 km²; wet season 13 km²) and made substantial upstream movements in the wet season (~15 km), presumably to explore new habitats and avoid competition with dominant males. Home range sizes for all age classes were most similar during the peak dry season (<3 km²) when hippos were most confined to water. These movement data are especially informative because they depict where in the landscape hippos are likely to have the greatest ecological impact. However, additional hippo tracking studies, with larger sample sizes that include females, are required to provide more comprehensive baseline information on hippo spatial ecology.

While hippo movements underpin the spatial extent of their impacts, they alone cannot tell us what the actual impacts of hippos are on vegetation. Thus, ascertaining hippo grazing impacts, and fully revealing their dietary flexibility, requires alternative approaches. One approach to investigate this has been the use of enclosure experiments. To our knowledge, only three studies have attempted this approach for hippos specifically (O'Connor & Campbell, 1986; Verweij *et al.*, 2006; McCauley *et al.*, 2018), and this handful of experiments represent most of what we currently know about hippo impacts on grazing systems. Together, these studies demonstrate that near water, and during particular times of year, hippos create and maintain productive short-grass ecosystems, and suppress woody plant height in regularly grazed areas (Verweij *et al.*, 2006; McCauley *et al.*, 2018). Further advances in hippo enclosure experimental design could be made by applying enclosures at varying distances from water to determine at what distance away from water hippo grazing impacts become diluted or disappear entirely. Furthermore, although hippos are widely considered grazers (Scotcher *et al.*, 1978), evidence from enclosure experiments (McCauley *et al.*, 2018) and dietary

studies suggest that they also incorporate forbs and woody material into their diet (Cerling *et al.*, 2008; Chritz *et al.*, 2016). Uncovering the dietary flexibility of hippos, and thus their impact on plant communities, may be especially relevant given the increasing prevalence and severity of drought, thus reducing grass availability for hippos and other herbivores (Chritz *et al.*, 2016; Utete *et al.*, 2017; Smit *et al.*, 2020). Approaches such as dietary DNA metabarcoding (De Sousa, Silva & Xavier, 2019), could be useful in revealing flexibility of hippo diets across seasons and in different habitats (Subalussy & Post, 2018).

The role of environmental context on hippo ecosystem engineering is also poorly understood (Dutton *et al.*, 2020). The magnitude and direction of hippo impacts appears to be highly dependent on characteristics of their aquatic habitat. Thus, as with elephants and other megaherbivores, hippo ecological impact is likely contingent on environmental factors. For instance, habitats with large water volumes (e.g. perennial rivers, dams and lakes) enable hippos to aggregate in greater numbers but at lower local densities. Larger expanses of water also dilute dung inputs, reducing the potential for nutrient overload and eutrophication of water bodies. By contrast, habitats characterised by smaller water volumes (e.g. non-perennial rivers, seasonal pans) restrict hippos to smaller and more isolated aquatic habitats (Stommel *et al.*, 2016), but likely concentrate their nutrient additions and facilitate the accumulation of dung and nutrients at levels that can be harmful to other organisms, as well as spatially restricting their grazing. Similar comparisons can be made across or within regions that differ in rainfall patterns over space and time. The increased prevalence and severity of drought across Africa (Gizaw & Gan, 2017; Ahmadiyoun *et al.*, 2019; Haile *et al.*, 2020) might alter the relationship that hippos have with their environment. As many ecosystems become hotter and drier, hippos will likely be forced to move further away from water to find suitable grazing, increasing the likelihood of human–hippo encounters. During times of drought, people are also likely to be more desperate and less tolerant of interactions with hippos, e.g. crop raiding, further escalating conflict. Therefore, gradients of aridity are likely important determinants of hippo ecosystem engineering and a key driver of human–hippo conflict severity. Future research aimed at determining the validity of this hypothesis, as well as how other environmental factors might drive variability in the ecological and social impacts of hippos, is warranted.

VII. CONCLUSIONS

(1) Hippo morphology and natural history determine their unique ecosystem impacts, which we postulate are more diverse than any other extant megaherbivore (Table 1, Fig. 4). Because hippos are semi-aquatic, they serve as important aquatic–terrestrial linkages, *via* their transboundary

transport of nutrients, and *via* the pathways and channels they create between land and water.

(2) Due to their considerable impact in both terrestrial and aquatic ecosystems, no other megaherbivore is capable of fully replicating the ecological roles of hippos. Nonetheless, across broad landscapes that do not have suitable hippo habitat, hippos likely have minimal influence. Here, terrestrial megaherbivores that are less constrained by water and still have relatively healthy populations, e.g. elephants and giraffes (Table 1), probably engineer considerably larger areas than hippos.

(3) However, at local scales and in areas of suitable hippo habitat, we postulate that hippos impact their environment more intensively, albeit in sometimes cryptic ways. Hippos are infrequently observed grazing even though they consume vast quantities of vegetation. Water quality and other metrics of aquatic health and diversity impacted by hippos are possibly less conspicuous than terrestrial impacts, but no less important.

(4) Ecosystems experiencing severe declines in hippo populations, or where hippos have been eradicated entirely, are likely to be significantly poorer ecologically. For instance, a lack of short-grass grazing lawns along rivers where hippos have been extirpated could increase fire prevalence along river banks, suppressing fire-sensitive riparian woody species.

(5) Fewer 'hippo lawns' are likely to attract fewer mesoherbivores, reducing the hippo's facilitative role, and potentially increasing predation rates as herbivores lack open areas in which to take refuge from predators, but still need to come to water to drink.

(6) Nutrient transfer between land and water is critical for stimulating aquatic productivity, and without such nutrient addition by hippos, the abundance and diversity of aquatic life will be diminished.

(7) Even within areas that have seemingly intact hippo populations, hippo abundance is likely consequential for determining their overall ecosystem engineering influence, and conservation managers should seek to ensure that landscapes sustain healthy hippo populations that lead to a diverse array of ecosystem influences.

(8) Human activities have a strong capacity to alter the outcome of hippo ecosystem engineering by altering water availability, flow rates and water quality, which can lead to alternative ecosystem responses. For example, water extraction and nutrient runoff from agriculture in conjunction with hippo nutrient additions can lead to eutrophication of aquatic environments.

(9) Hippos have received less conservation and scientific attention than other megaherbivores. Yet, hippo populations are becoming increasingly vulnerable to both natural and human-induced threats. Of particular concern is habitat loss and increasing human–hippo conflict due to expansion of agriculture and human activities onto floodplains, mismanagement of freshwater ecosystems, and increased drought prevalence, which can have a negative influence on hippo population stability.

(10) If such trends continue, much is at stake for African landscapes. Ecosystem functions driven in large part by

hippos could be lost should the species disappear from certain areas. We encourage greater consideration of hippos and their unique role as ecosystem engineers when considering the functional importance of megafauna.

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