Chapter 8
Herbivory: Mammalian Grazers and Browsers

Key Concepts and Questions: This Chapter Explains

- *How soils, climate, fires and mammalian herbivores evolved and interacted to shape Angola's vegetation and animal communities.*
- *Why soils and the nutritional quality of vegetation they carry influence the patterns of herbivore impacts in African ecosystems.*
- *What factors determine the distribution and structure of Angola's mammal herbivore communities.*
- *How the impacts of grazing cattle and browsing goats have replaced those of indigenous herbivores.*

Context: The Coevolution of C$_4$ Grasses, Savannas, Herbivores and Humans

> Herbivores are a main driver of ecosystem patterns and processes in semi-arid savannas, with their effects clearly observed when they are excluded from landscapes.
>
> (Wigley-Coetsee et al., 2022)

African ecosstems have endured and adapted to at least eight million years of regular fires across the highly flammable C$_4$ grasslands and fire-tolerant woodlands of its mesic/dystrophic savannas. Its arid/eutrophic savannas have co-evolved in the presence of a rich fauna of mammal herbivores, in particular the antelope that characterise Africa as a wildlife paradise. Climatically, Africa did not experience the dramatic episodes of glaciation that transformed the landscapes of Northern Hemisphere continents during the cold, dry Ice Ages of the Pleistocene. Neither did Africa witness the extinction of megaherbivores that occurred in Australia, the Americas, Madagascar and New Zealand (Owen-Smith, 1987, 2021) over the last 40 thousand years, as *Homo sapiens* the hunter/gatherer expanded across the globe from the savannas of eastern and southern Africa—the Cradle of Humankind. The happy coincidence of the early evolution of *H. sapiens* on the savannas of Africa is possibly the reason why the modern large herbivores of Africa were able to co-evolve with the human species. The mammals could adapt to human hunting pressures over many tens of

thousands of years, rather than collapse as they did on the other continents, where the encounter was comparatively rapid.

More recently, during the past 10,000 years, domesticated cattle and goats have been introduced to Africa from Eurasia. Their impact on Africa's rangelands has been dramatic. A synopsis of the role of indigenous mammal herbivores (largely free-roaming) in shaping the vegetation of the savannas, and the changes brought about by the introduction by human societies of domestic grazers and browsers (largely sedentary) to Africa provides insights to the changing patterns of herbivory across the continent.

Herbivores, whether grazers or browsers, have both negative and positive impacts on the plants on which they feed. Herbivores can:

- Stimulate grass growth, or be destructive of plants.
- Contribute to nutrient cycling.
- Maintain or change the relationship between grass and woody plant density.
- Open the canopy of grasses and trees.
- Reduce the rate of fuel accumulation and thus of fire intensity.
- Retard or accelerate the pace of recovery from defoliation.

Herbivores range in size from the smallest invertebrates to the largest of land mammals. In mesic/dystrophic savannas of central and western Africa the biomass of vertebrate herbivores is much lower than in the arid/eutrophic savannas of eastern and southern Africa. In the mesic savannas, earthworms, termites and decomposing microorganisms, together with fire, occupy the role of the large herbivorous mammals of arid savannas. The close evolutionary relationships between herbivores and the plants they depend on and the landscapes they inhabit, account for the diversity of the herbivore communities across Africa.

8.1 The Evolution of African Mammalian Herbivores and of Arid/Eutrophic Savannas

Our understanding of the distribution and density of the African fauna, like that of its flora, has progressed from the oral accounts of traditional communities, and the documented observations of naturalists of the colonial era, to the more objective and data-rich syntheses of the past decades. While the century-old biome concept has recently been widely applied for African vegetation formations (Burgess et al., 2004), new concepts such a pyromes (Archibald et al., 2013) and herbivomes (Hempson et al., 2015a) have been proposed for the collective characteristics of fires and herbivores. These are useful conceptual frameworks, and will help guide an understanding of the role of mammalian herbivores in shaping Angola's biomes.

Plant responses to herbivory have long been recognised, but the distinction between the patterns of response to fires and herbivory in arid/eutrophic and mesic/dystrophic savannas has been blurred by many studies that treat all African

Fig. 8.1 Diversification of spiny plant and bovid (including antelope) lineages in Africa. From Charles-Dominique et al. (2016) *Proceedings of the National Academy of Sciences*, 113(38), E5572–E5579
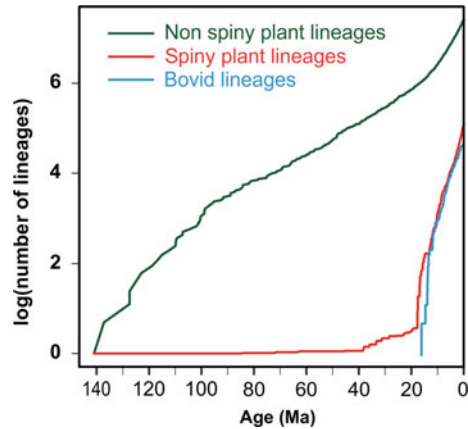
savannas as a single biome. Recent research by Bond (2019 and references therein) has brought convincing phylogenetic, paleoecological and ecological evidence that informs an understanding of the long history of the distinctive evolutionary pathways of the two African savanna biomes.

The key feature of tropical savannas (their C_4 grasses, evolved in response to fire and seasonal drought) made their appearance ca. 30 Ma, with the rapid expansion to their current prominence dating from ca. 8 Ma. The disjunction between the mammalian herbivore-dominated arid/eutrophic savannas, and fire-dominated mesic/dystrophic savannas (Archibald et al., 2017; Huntley, 1982), might date from the mid-Miocene (ca. 16 Ma). This was when stem spines appeared on woody plants (to reduce browsing) and the diversification of African bovids accelerated (Charles-Dominique et al., 2016; Fig. 8.1). The thornless mesic savannas probably evolved later. They were well established before the origin of geoxylic suffrutices, which are characteristic features of mesic savannas, and which date from the Pliocene, less than 5.3 Ma (Maurin et al., 2014).

Both woody plant **architecture** (spiny/non-spiny) and grass **nutrition quality** (high/low) are key features of different African savannas and their resultant herbivore composition. An important distinction between the grasses of African savannas is the differences in the proportions of their respective investment in metabolic (M) and structural carbohydrate (C) constituents (Bell, 1982). **Metabolic constituents** (proteins and soluble carbohydrates) are what **herbivores** require for growth. **Structural carbohydrate constituents** (cellulose, hemicellulose and lignin) are what **grasses** require for growth. The ratio of M/C determines the value of herbage to herbivores. Plant-available soil nutrients determine the ability of grasses to produce protein, while water limits the total biomass of the end product of grass growth. The consequences of the different soil nutrient conditions in the two savanna biomes are summarised in Table 8.1.

The fire/herbivory interactions in arid and mesic savannas are typical of nature's feedback systems which maintain ecosystem equilibria and include:

Table 8.1 Characteristics of the grass cover of arid/eutrophic and mesic/dystrophic savannas

Arid/eutrophic savannas	Mesic/dystrophic savannas
• Grasses have high nutrition value	• Grasses have low nutrition value
• Low rainfall/low grass biomass	• High rainfall/high grass biomass
• High herbivore biomass controls grass structure	• Low herbivore biomass has low impact on grass cover
• Mixed feeders	• Selective or bulk feeders
• Limited combustible material	• High biomass of combustible fuel
• Infrequent fires	• Frequent fires

- A high proportion of palatable arid savanna grasses being consumed by herbivores, with less fuel for fire;
- A high proportion of unpalatable grasses in mesic savannas, with low levels of herbivory, providing more fuel for fires.

The mechanisms involved in these interactions have been demonstrated in arid and mesic ecosystems of Kruger National Park (Smit & Archibald, 2019) and are relevant to similar systems in Angola. The evolutionary responses of mammalian herbivores to these and other food quality challenges are well illustrated by adaptations of their digestive systems (Box 8.1).

Box 8.1 The Ruminant Gut and Hypsodont Teeth: Succeeding on Low Quality Forage

The most successful mammalian herbivores are the ruminants, which include members of the bovidae, giraffidae and tragulidae. The bovidae include 35 species indigenous to Angola (including, for example, Impala, Springbok, Giant Sable, Greater Kudu and Forest Buffalo), with one species each of giraffe and tragulid. The Angolan Giraffe (*Giraffa giraffa angolensis*) was once the symbol of Mupa National Park, but is now extinct in Angola. The tragulid (Water Chevrotain *Hyemoschus aquaticus*) known from Cabinda and Uíge, is an ancient, ancestral species related to the first small, forest-dwelling ruminants that evolved 50 million years ago. Little is known of the ecology of this elusive mini-ungulate of the Maiombe and Uíge forests. Currently the most numerous ruminants in Angola, and the world, are domestic cattle, sheep and goats, with a massive global population of 3.6 billion, which is orders of magnitude more abundant than indigenous ruminant species.

The rapid speciation of ruminants can be explained by the adaptations to life on the grasslands and open savannas of Africa during the arid Miocene (Chap. 4, Box 4.1). However, the early mammal herbivores faced two challenges. First: the fire-tolerant C_4 grasses that dominate tropical savannas have high **cellulose** and **silica** contents. To digest cellulose a special enzyme, **cellulase**, is needed,

but is absent in mammals. Second: the teeth of early mammalian herbivores were rapidly worn down by the gritty grasses. Two evolutionary responses evolved.

- First, mutualistic relationships evolved with **microorganisms** (bacteria, protozoa and fungi) that have cellulases that facilitate digestion in the herbivore stomach. These microorganisms break down the cellulose to fatty acids, proteins and sugars, essential for energy and growth. This mutualism solved the first challenge.
- Second, the problem of gritty grasses was addressed by the evolution of high-crowned (**hypsodont**) teeth covered with enamel—the hardest material in nature—extending past the gum line, greatly reducing wear and tear. These grinding molars were adapted to masticate the coarse grass leaves and stalks, and prepare rough plant material for digestion.

Grasses, in response to grazing by herbivores, evolved **intercalary meristems**. These are the growing points in grass stems and at the base of grass leaves that allow rapid growth after damage, such as that caused by frequent grazing. Grasses also have the meristematic tissue of their main shoots (**tillers**) located at the soil surface (**basal tillering**), providing protection against fire and intense grazing. Most savanna grasses form multi-tiller tussocks, which might live for many decades. Grasses depend on regular defoliation (by grazers or fire) to stimulate growth. Too much grazing and trampling pressure can damage the meristems and cause death. Too little defoliation can result in a dense mat of fire-prone dead grass shading and ultimately killing the grass plant. It has been suggested that fire, grasses (with basal tillering and intercalary meristems), and antelope (with hypsodont dentition and slender, hoof-tipped legs, ideal for fast escape from predators in open grasslands), coevolved during the rapid expansion of savanna through the Miocene/Pliocene (Box 4.1).

It is important to note that the ungulates (hooved mammals) fall into two distinct groups—the even-toed ungulates (**artiodactyles**—pigs, hippopotamus, antelope) and the odd-toed ungulates (**perissodactyles**—zebra, rhinos). Ungulates are furthermore grouped according to two different digestive systems—hindgut fermentation and foregut rumination.

Artiodactyles (with the exception of pigs and hippos) are **ruminants**, which require relatively high-quality food. Perissodactyles are **hindgut fermenters** which can make use of low-quality food. The two digestive systems are illustrated in Fig. 8.2.
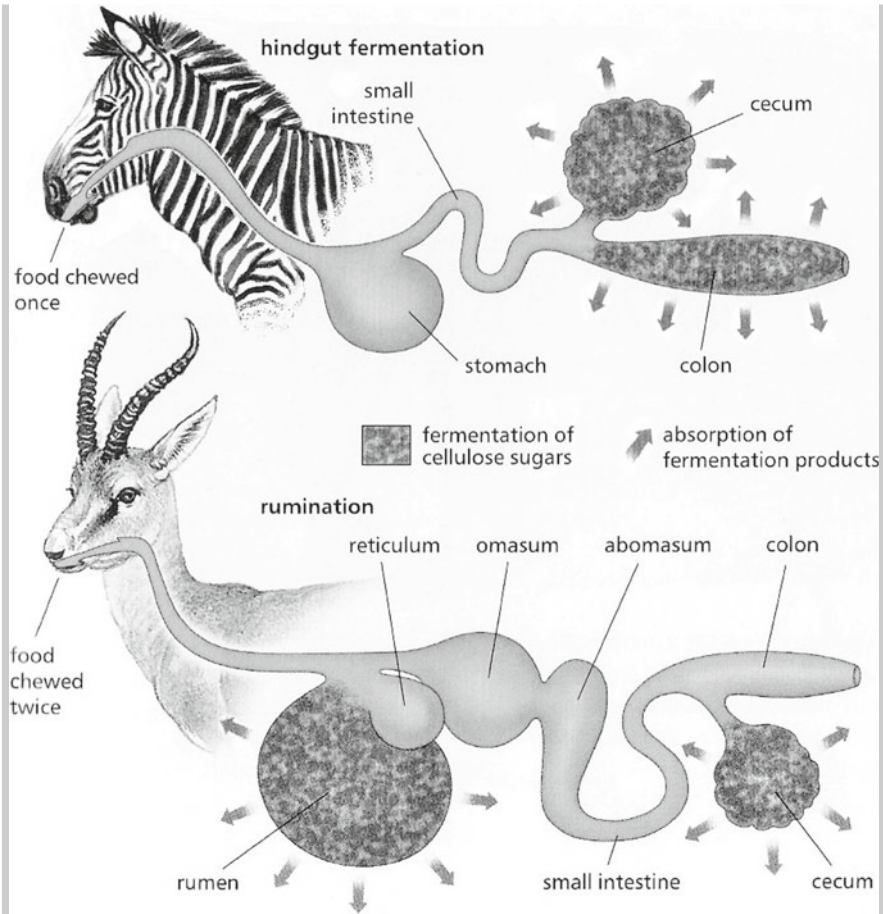
Fig. 8.2 Stylised comparison of hindgut fermentation and rumination digestive systems. From Shorrocks (2007) *The Biology of African Savannahs*. Oxford University Press, Oxford

- In hindgut fermenters (which include elephant as well as zebra and rhino), the food is chewed once and passed to the stomach where it is digested. It then is passed to the caecum and colon, where it is fermented by microorganisms. This process is only 50% effective in digesting cellulose, but because it is a comparatively simple throughput, it is fast, completed in 48 h. The dung of hind-gut digesters is rough, reflecting the poor breakdown of celluloses.
- Ruminants (excluding the primitive Chevrotain) have a four-chambered stomach. Food is consumed, chewed with a mix of saliva, and enters the first chamber—the **rumen**. The rumen acts as a storage compartment, allowing continued processing of food long after it is consumed. The

coarsest parts of the plant material (the **cud** or **bolus**) are then regurgitated back into the mouth where they are once again chewed (chewing the cud) a process known as **rumination**. Passed back to the rumen, it is fermented by microbial activity. This material is then passed to the second chamber—the **reticulum**. Here it is further fermented, and passed to chamber three—the **omasum**, where it is filtered. Hereafter it passes to the fourth chamber, the **abomasum**—the 'true stomach'—and to the **small intestine** and on to the **caecum**, where further digestion and absorption occurs. This complex process takes about 80 h, but is 80% effective in breaking down (**hydrolysing**) the cellulose and other nutrients contained in the rough plant material. The dung of ruminants is consequently fine-grained.

The minimum level of protein required by ruminants to maintain microfloral activity is 6%. Despite the selection of relatively high-quality forage, the slow digestion process of ruminants has a serious constraint. If the protein level drops below 6% (frequent in the mesic/dystrophic savannas of the miombo) the slow processing of their food can lead to the loss of weight and physical condition. Despite the high primary (plant) productivity of low nutrient mesic savannas, they cannot carry a proportionate (herbivore) productivity. In contrast, the arid/eutrophic savannas, with sustained protein content, can carry a much higher ungulate biomass than the mesic savannas.

The coevolution of C_4 grasses, hypsodont teeth and rumination accounts for the success of savanna herbivores across Africa.

8.2 The Herbivomes of Africa

South African ecologist Gareth Hempson and co-workers undertook an ambitious synthesis of the biomass and **functional traits** of 92 species of African mammal herbivores. Together with rainfall, fire regime, biome and soil data they delimited herbivory regimes which, following the language of biomes and pyromes, they called herbivomes (Hempson et al., 2015a). Their five **functional types** (Fig. 8.3) and four **herbivomes**, provide conceptual frameworks that are highly relevant to understanding the distribution patterns of Angola's mammal herbivores. The concept of functional type (or functional trait) is used by ecologists to simplify the structure of communities into manageable units for study and to answer basic questions on their relationships with other species and the environment. All five functional types and four herbivomes are represented in Angola.
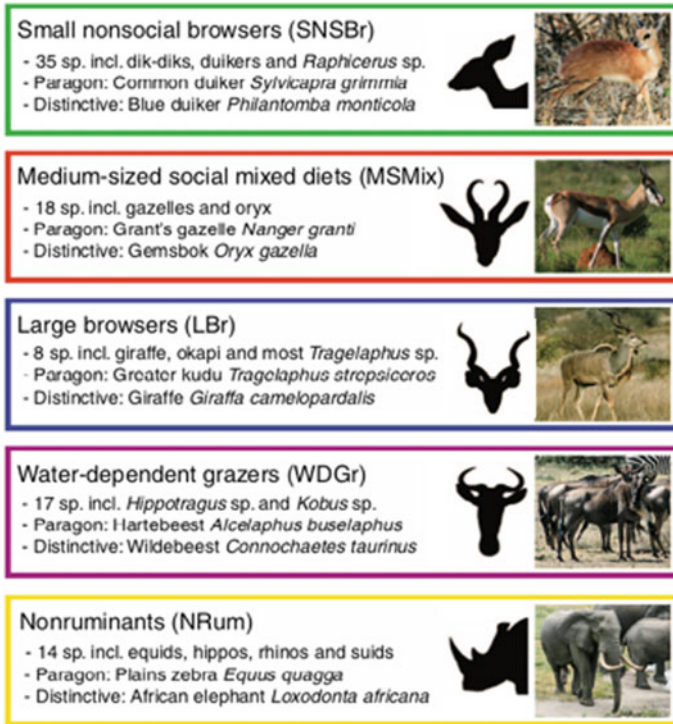
Fig. 8.3 Herbivore functional type classification for African mammals. From Hempson et al., (2015a) *Science*, 350(6264): 1056–61

Functional Types

- The **small, non-social browser** functional type is characteristic of the antelope of the moist closed forests of Cabinda, Zaire, Uíge and Lunda-Norte (Bay Duiker, White-bellied Duiker, Black-fronted Duiker, Blue Duiker; Water Chevrotain). This group of small, non-social browsers also includes the Dik-dik and Steenbok of the arid southwest.
- The **medium-sized, social mixed feeders** are arid savanna species (Springbok, Gemsbok).
- **Large browsers** (Greater Kudu, Giraffe) are also arid savanna species.
- **Water-dependent grazers** include both arid and mesic savanna species (Blue Wildebeest, Sable, Roan, Lechwe, Puku).
- The fifth group includes **the non-ruminants** (Zebra, Black Rhinoceros, Savanna and Forest Elephant) that because of their ability to utilise rough, nutrient-poor herbage are characterised as bulk-feeders.

The distribution of herbivore biomass according to functional type in Africa is overwhelmed by the non-ruminant group, where elephant alone exceed the biomass

Fig. 8.4 Distribution of African large mammal herbivomes. From Hempson et al., (2015a) *Science*, 350(6264): 1056–61
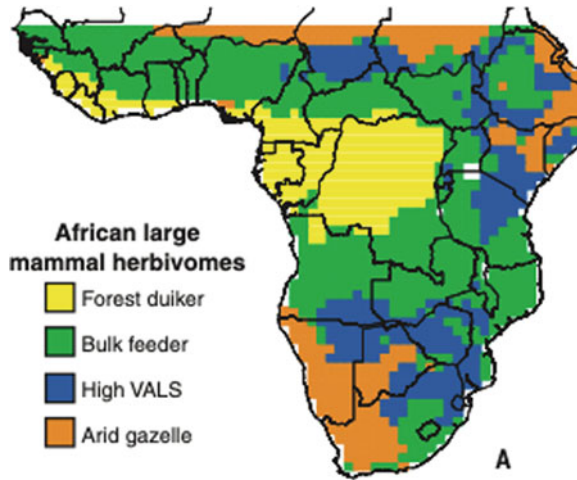
of all other 91 herbivore species combined (Hempson et al., 2015a). Fritz et al. (2002) demonstrate that the biomass of megaherbivores, in particular elephant, is limited by food quantity, not by food quality, due to their ability to tolerate low quality food in higher rainfall areas with low fertility soils.

Herbivomes

A cluster analysis of the data-set compiled by Hempson and colleagues revealed four **herbivomes** based on functional type, social behaviour and habitat (Fig. 8.4).

- The **'forest duiker' herbivome** fits with the forested habitats of central and west Africa, including northern Angola.
- The **'arid gazelle' herbivome** matched the arid savannas of southwest Africa, the Horn of Africa and the Sahel.
- The third, and largest distinct group is the **'bulk feeder' herbivome**, with distributions fitting with the mesic/dystrophic savannas (including miombo). The bulk feeder herbivome comprises a high proportion of water-dependent non-ruminant grazers, but with elephants making the largest contribution to overall biomass. The habitat of this group is largely confined to low nutrient soils, where grasses are of low nutrition value, produce high biomasses of fuel, and where fire rather than herbivory is the main consumer.
- The fourth grouping is the **'high variety and abundance of larger species' herbivome (VALS)**. This group includes the arid/eutrophic savannas of Africa, especially those of nutrient rich soils and consequently more nutritious herbage.

In southern Africa, this fourth 'VALS' herbivome includes the floodplains and adjoining open savannas of the Cuando Cubango/Okavango, and the arid savannas of Botswana, Zimbabwe and South Africa. In previous centuries it also included the arid coastal zone of Angola, from Namibe to Benguela and even Luanda, where remnants of a once abundant large herbivore fauna survived in Quiçama until the 1970s. In

eastern Africa, it includes the basaltic Serengeti Plains. These are the epicenters of antelope diversity and abundance of the world and the sites of major national parks and World Heritage Sites such as Okavango, Kruger, Hwange, Gorongosa, Tsavo and Serengeti.

8.3   Patterns of Impacts of Browsers and Grazers

Africa today retains, at least in effectively managed protected areas, a megafaunal assemblage that resembles that of the Pleistocene. It is an ideal continent on which to study the role of mammal herbivores in ecosystem dynamics, especially in terms of their impacts on nutrient cycling, damage to trees, consumption of buds, seeds and leaves, the dispersal of fruit and the opening up of woodlands by trampling.

Herbivores (specialist consumers) also act as competitors with fire (a generalist consumer) by consuming potentially combustible fuel, thus reducing fire intensity and impact. At high densities, browsers create a distinct browse line in trees and shrubs, at levels proportionate to their reach. If they remove the growing tips of tree saplings, the combined effects of browse and fire will cause mortalities and possibly a change in vegetation structure. Tree saplings have to outpace both the **fire trap** and the **browse trap** to reach maturity (Chap. 10, Fig. 10.14).

In some areas, herbivores might maintain open savanna where the climatic potential is forest, although evidence of such herbivore-mediated controls in high rainfall areas is limited. Herbivore-constrained savanna structure is rare in moist and mesic savannas, which are notorious for their very low herbivore biomass. Conversely, in arid savannas, herbivores exert significant controls on vegetation structure. Mega-herbivores (body mass greater than 1000 kg) such as elephant might cause physical damage to large trees, and reduce a tall woodland to a short shrubland. In Kruger National Park, herbivore exclusion over 22 years revealed an 11-fold greater woody canopy cover in areas without herbivores when compared with sites exposed to mammalian herbivores (Asner et al., 2009). The long-term herbivore-exclosure experiments in an arid/eutrophic *Colophospermum* savanna in Kruger National Park (Wigley-Coetsee et al., 2022; Figs. 8.5 and 8.6) demonstrate the impact of elephant on vegetation structure. Similar impacts were not noted in exclosures in mesic/dystrophic savannas with the same elephant densities (Asner & Levick, 2012). Mega-grazers, such as Hippopotamus and White Rhinoceros can also open up dense grass and shrub cover, establishing '**grazing lawns**' (Hempson et al., 2015b). Waldram et al. (2008) describe White Rhinoceros as ecological engineers due to their top-down effects on ecosystem structure, creating a mosaic of fire-free patches of short, nutritious lawns, thereby facilitating the habitat's use by other herbivore species.

Owen-Smith (1982, 2021) notes the distinction between browsers (which select plant species and plant parts for maximum **energy** gain), and grazers (that focus on plant quality, for maximum **nutrient** gain). Whereas *Colophospermum mopane* (mopane/mutiati) has no structural defences against herbivory, many woody species

Fig. 8.5   Elephant damage to *Colophospermum mopane* arid/eutrophic savanna in Kruger National Park. *Photo* Merle Huntley

Fig. 8.6   Mopane woodland protected from elephants within a large exclosure. *Photo* William Bond

of arid/eutrophic savannas do, such as the spinescent adaptations of genera such as *Acacia, Adenium, Balanites, Capparis, Dichrostachys, Euphorbia, Gymnosporia, Maytenus* and *Zizyphus*. Such defences do not always prevent herbivores from consuming leaves and shoots, but reduce the rate and volumes removed per unit effort. These plants, and the mammals that feed on them, have co-evolved.

Mammals that browse on spiny trees and shrubs have narrower muzzles, longer tongues, and prehensile lips, allowing them to handle thorny plants better than broad-mouthed grazing species. An instructive comparison is that of the two African rhino species. The Black Rhinoceros (also known as the prehensile-lipped rhino) is a browser while the White (or Square-lipped Rhino) is a grazer. The two species have distinctive feeding habits and ecological impacts. Black Rhino consume thorny shrubs, opening up thickets. White Rhino graze grasses into distinctive 'grazing lawns', which maintain fire-free areas.

The tallest of antelope, Giraffe, which usually have limited impacts on habitat structure, can exert serious damage to arid savanna species if the density of giraffes exceeds the carrying capacity of the tree community (Bond & Loffell, 2001). After giraffe were introduced into the Etendeka Concession in northwest Namibia, they caused the local suppression of their preferred browse (*Maerua* and *Boscia*) and the disappearance of some bird species (Christopher Hines, pers. comm. 2020). This situation can even arise at low densities of Giraffe (and other herbivores) where low browse availability results from drought or high levels of competition.

While elephants have the physical capacity to transform woodlands to shrublands, so too do porcupines, at the opposite end of the herbivore biomass spectrum. Yeaton (1988) describes a sequence of porcupine damage to the basal bark of *Burkea africana* trees, followed by repeated fire damage to the exposed xylem, and finally the collapse of the trees during windstorms. The process developed over a 20-year sequence of four or five fires, each fire burning deeper into the damaged trunk, and resulting in up to two percent of the large trees being felled per year. In mesic/dystrophic savannas such as those dominated by *Burkea africana*, with low soil nutrient status and very slow tree growth, even a two percent per annum mortality can have significant impact on woodland structure.

Box 8.2 Human–Environment Interactions: The Transformation of Savannas by Domestic Livestock

We live in a world that has been greatly transformed by human activities, especially over the last two centuries of industrialisation (the **Anthropocene**). Such changes were preceded by changes throughout the late Pleistocene—especially over the last 40,000 years—as described in the introduction to this chapter. As human-driven ecological transformations intensify through the Anthropocene, focus has been directed towards the progressive socio-economic impacts of global warming anticipated within the present century (Box 5.1). But in Africa, far more rapid changes have occurred during the past century through distortions to the structure and biomass of herbivores as a result of

agriculture, grazing, and deforestation. In a series of studies embracing sub-Saharan Africa, Hempson and colleagues have synthesised a vast data base on the mammalian herbivores (both indigenous wildlife and introduced livestock) of the region (Archibald et al., 2013; Archibald & Hempson, 2016; Hempson et al., 2015a, 2017). These authors have made remarkable and important findings. By comparing geo-referenced current and historic herbivore communities, based on species-level biomass data, with data on fire frequency, herbivore impact and soil characteristics, they demonstrate substantial total mammalian biomass losses in mesic savannas and biomass increases in arid savannas. They relate these changes to a range of environmental pressures (hunting, rainfall, fire and the increase of domestic livestock).

Pastoral traditions with domestic livestock (cattle, sheep, goats) have been practiced across Africa for at least 2000 years, and the numbers of individuals and the total biomass of domestic species now greatly exceed those of indigenous species. Domestic livestock strongly modify ecosystems through effects on fire frequency and intensity, tree cover and nutrient dispersal. Domestic livestock also compete directly with indigenous herbivores for the most nutritious grazing. Livestock biomass currently matches or exceeds past wildlife biomass (excluding elephant) in areas with rainfall up to 1000 mm per year (Hempson et al., 2015a; Fig. 8.7). In areas receiving more than 1000 mm MAP, the biomass of livestock falls below that of former wildlife biomass levels.
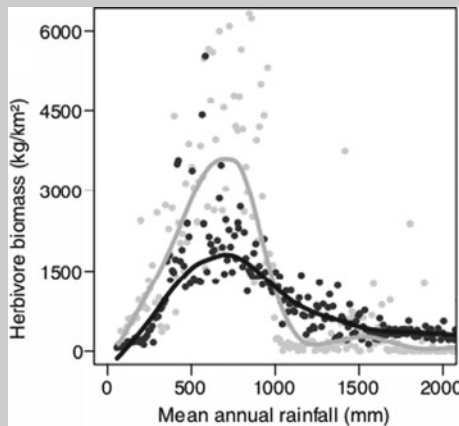
Fig. 8.7 Herbivore biomass in relation to mean annual rainfall. Both reconstructed past indigenous herbivore biomass (excluding elephants)—(black points and line) and present livestock biomass (grey points and line) peak at ca. 650–750 mm mean annual rainfall, where arid/eutrophic savannas and mesic/dystrophic savannas interdigitate. From Hempson et al., (2015a) *Science*, 350(6264): 1056–61

Current domestic livestock populations exceed past wildlife biomass in arid savannas, where the provision of supplementary water and fodder

has boosted carrying capacity and removed a key constraint on herbivore numbers—as determined by the interannual variability in water and food availability. Hempson et al. (2017) demonstrate that above a biomass threshold of 1500 kg km^2, herbivores reduce grass accumulation and thus increase fire suppression. This situation is true in Angola, both in arid savannas (Cunene, Namibe, Benguela) and on the margins of mesic savannas (Huíla) where intensive pastoral systems have been developed over the past century. Whereas indigenous mammal numbers fluctuate widely in response to the variability of resources, domestic livestock numbers tend to be pegged to the pastoralist's perception of average conditions defined by traditional stocking rates.

A consequence of heavy grazing, and the reduction of fuel load for fire, is that of thicket formation (**bush-encroachment**) in many parts of southern Africa. Spiny *Acacia* species and *Dichrostachys cinerea* are particularly prone to such thicket formation where fire has been suppressed by overgrazing. However, after episodes of high rainfall and rapid growth of annual grass species, and the accumulation of fuel followed by rare but hot fires, the seeds of *Dichrostachys cinerea* are known to germinate rapidly. Fire is thus both a stimulant of seed germination, and a suppressor of seedling development, interacting in complex ways with herbivores.

In contrast to the arid savannas, over most of the mesic/dystrophic savannas (miombo), past and present livestock biomass remains low due to the nutrient-poor herbage on heavily leached and low nutrient soils, and to the presence of diseases such as trypanosomiasis.

Both Savanna and Forest elephants historically exerted strong impacts on woody vegetation, but the dramatic contraction of elephant range and population sizes over recent decades has resulted in measurable increases in woody cover (Stevens et al., 2016). The change results directly from reduced tree damage by browsing elephants, and indirectly through reduced opening of wooded communities to grass growth and thus increased fire penetration and damage to trees. Conversely, increasing goat populations in arid savannas have suppressed woody plant growth in some areas due to their negative impact on seedling establishment.

Long-term impacts of the distortion of the herbivore profile in Africa have included changes to patterns of nutrient dispersal due to the corralling of livestock at night to protect them against predators. Indigenous herbivores disperse nutrients over a wide area while domestic livestock, though corralling, concentrate nutrients in confined areas. Such nutrient hotspots can have significant effects on ecosystem structure, even at fine spatial scales. In *Burkea africana* mesic/dystrophic savanna at Nylsvley in South Africa, the sites of Middle Iron Age pastoral villages are reflected in pockets of *Acacia tortilis* arid/eutrophic savanna within the broad matrix of mesic/dystrophic *Burkea africana* savanna. The accumulation of nutrients from domestic livestock corralling resulted in a change in soil chemistry and texture, a change in vegetation structure and

composition, and a change in bird communities which persisted for hundreds of years after the corrals had been abandoned (Scholes & Walker, 1993). Extended across sub-Saharan Africa, the impacts of such changes in nutrient diffusion (estimated by Hempson et al. (2017) to have been reduced to 5% of past levels) could introduce novel distortions to ecosystem patterns.

Africa is thus unique in its richness of indigenous ungulates, and the close interactions these have with the diversity of biomes, ecoregions and ecosystems that have evolved in parallel for millions of years. The continent is also unique in the extended history of the co-evolution of *Homo sapiens*, the fire-maker and pastoralist, over many tens of thousands of years more than in any other continent.

References

Archibald, S., Lehmann, C. E., Gómez-Dans, J. L., et al. (2013). Defining pyromes and global syndromes of fire regimes. *Proceedings of the National Academy of Sciences, 110*(16), 6442–6447.

Archibald, S., & Hempson, G. P. (2016). Competing consumers: Contrasting the patterns and impacts of fire and mammalian herbivory in Africa. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 371*(1703), 20150309.

Archibald, S., Beckett, H., Bond, W. J., et al. (2017). Interactions between fire and ecosystem processes. In J. P. M. G. Cromsigt, S. Archibald, & N. Owen-Smith (Eds.), *Conserving Africa's mega-diversity in the Anthropocene* (pp. 234–261). Cambridge University Press.

Asner, G. P., Levick, S. R., Kennedy-Bowdoin, T., et al. (2009). Large-scale impacts of herbivores on the structural diversity of African savannas. *Proceedings of the National Academy of Sciences of the United States of America, 106*(12), 4947–4952.

Asner, G. P., & Levick, S. R. (2012). Landscape-scale effects of herbivores on treefall in African savannas. *Ecology Letters, 15*(11), 1211–1217.

Bell, R. H. V. (1982). The effect of soil nutrient availability on community structure in African ecosystems. In B. J. Huntley & B. H. Walker (Eds.), *Ecology of tropical savannas* (pp. 193–216). Springer.

Bond, W. J. (2019). *Open ecosystems: Ecology and evolution beyond the forest edge* (p. 191). Oxford University Press.

Bond, W. J., & Loffell, D. (2001). Introduction of giraffe changes acacia distribution in a South African savanna. *African Journal of Ecology, 39*(3), 286–294.

Burgess, N. D., Hales, J. D., Underwood, E., et al. (2004). *Terrestrial ecoregions of Africa and Madagascar—A conservation assessment* (p. 499). Island Press.

Charles-Dominique, T., Davies, T. J., Hempson, G. P., et al. (2016). Spiny plants, mammal browsers, and the origin of African savannas. *Proceedings of the National Academy of Sciences, 113*(38), E5572–E5579.

Fritz, H., Duncan, P., Gordon, I. J., et al. (2002). Megaherbivores influence trophic guilds structure in African ungulate communities. *Oecologia, 131*(4), 620–625.

Hempson, G. P., Archibald, S., & Bond, W. J. (2015a). A continent-wide assessment of the form and intensity of large mammal herbivory in Africa. *Science, 350*(6264), 1056–1061.

Hempson, G. P., Archibald, S., Bond, W. J., et al. (2015b). Ecology of grazing lawns in Africa. *Biological Reviews, 90*, 979–994.

Hempson, G. P., Archibald, S., & Bond, W. J. (2017). The consequences of replacing wildlife with livestock in Africa. *Scientific Reports, 7*(1), 17196.

Huntley, B. J. (1982). Southern African savannas. In B. J. Huntley & B. H. Walker (Eds.), *Ecology of tropical savannas* (pp. 101–119). Springer.

Maurin, O., Davies, T. J., Burrows, J. E., et al. (2014). Savanna fire and the origins of the 'underground forests' of Africa. *New Phytologist, 204*(1), 201–214.

Owen-Smith, N. (1982). Factors influencing the consumption of plant products by large herbivores. In B. J. Huntley & B. H. Walker (Eds.), *Ecology of Tropical Savannas* (pp. 359–404). Springer.

Owen-Smith, N. (1987). Pleistocene extinctions: The pivotal role of megaherbivores. *Paleobiology, 13*, 351–362.

Owen-Smith, N. (2021). *Only in Africa* (p. 350). Cambridge University Press.

Scholes, R. J., & Walker, B. H. (1993). *An African savanna: Synthesis of the Nylsvley study*. Cambridge University Press, Cambridge.

Shorrocks, B. (2007). *The biology of African savannahs* (p. 279). Oxford University Press.

Smit, I. P. J., & Archibald, S. (2019). Herbivore culling influences spatio-temporal patterns of fire in semi-arid savanna. *Journal of Applied Ecology, 56*, 711–721.

Stevens, N., Erasmus, B. F. N., Archibald, S., & Bond, W.J. (2016). Woody encroachment over 70 years in South African savannahs: Overgrazing, global change or extinction aftershock? *Philosophical Transactions of the Royal Society B, 371*(1703).

Waldram, M. S., Bond, W. J., & Stock, W. D. (2008). Ecological engineering by a mega-grazer: White rhino impacts on a South African savanna. *Ecosystems, 11*(1), 101–112. https://doi.org/10.1007/s10021-007-9109-9

Wigley-Coetsee, C., Strydom, T., Govender, D., et al. (2022). Reflecting on research produced after more than 60 years of exclosures in the Kruger National Park. *Koedoe, 64*(1), a1674. https://doi.org/10.4102/koedoe.v64i1.1674

Yeaton, R. I. (1988). Porcupines, fire and the dynamics of the tree layer of the *Burkea africana* savanna. *Journal of Ecology, 76*, 1017–1029.