

EFFECTS OF ELEPHANTS ON ECOSYSTEMS AND BIODIVERSITY

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On the following morning we were up before the sun, and, travelling in a northerly direction, soon became aware that we were in a district frequented by elephants, for wherever we looked, trees were broken down, large branches snapped off, and bark and leaves strewn about in all directions, whilst the impress of their huge feet was to be seen in every piece of sandy ground. *FC Selous (1881, 39), north of Gweru, Zimbabwe, in 1872*

INTRODUCTION

THE ISSUE of the effects of elephants within ecosystems has emerged strongly since the formulation of the concept of the 'elephant problem and the concerns that elephants may irrevocably alter the remaining areas which are available to them' (Caughley, 1976a). Two perspectives need to be kept in mind when these concerns are raised. Firstly, the order of Proboscideans (including the modern elephants) evolved in Africa as part of a unique group of mammals, the Afrotheria (Robinson & Seiffert, 2003), with their roots going back 80 million years. Proboscideans of various forms subsequently colonised all continents except for Australia and Antarctica; mammoths in the family Elephantidae remained abundant and widespread through most of Europe and North America until as recently as 12 000–16 000 years ago (Sukumar, 2003). The modern African elephant emerged about 3 million years ago. Hence, its relationships with other animal and plant species have been an integral part of the co-evolutionary history of the ecosystems and biodiversity of Africa.

Herbivores, through their consumption of plant tissues, affect the relative growth, survival and reproductive output of these plants, with consequences for vegetation structure, community composition and ecosystem processes (Huntly, 1991). Even relatively small herbivores can have profound effects in shaping ecosystem structure, particularly when they occur at high densities.

For example, Côté *et al.* (2004), writing about the increase in deer abundance, had the following to say:

They affect the growth and survival of many herb, shrub and tree species, modifying patterns of relative abundance and vegetation dynamics. Cascading effects on other species extend to insects, birds, and other mammals. Sustained over-browsing reduces plant cover and diversity, alters nutrient and carbon cycling, and redirects succession ... simplified alternative states appear to be stable and difficult to reverse.

Similarly, smaller herbivores with specific manners of feeding can alter ecosystems, although their abundance and overall use of resources are not great. Feeding by porcupines *Hystrix africaeaustralis* on the bark of red syringas *Burkea africana* exposes the xylem to fire, with consequent increases in tree mortality (Yeaton, 1988; De Villiers & Van Aarde, 1994). Granivory and seedling predation by rodents alters many plant communities (Brown & Heske, 1990).

Nevertheless, the feeding and breakage impacts of elephants on plants are greater in magnitude and scale than those of smaller herbivores, particularly through affecting the structural components of the vegetation like canopy trees (Owen-Smith, 1988). From this perspective elephants have been termed 'megaherbivores', along with other species exceeding 1 000 kg in adult body mass with similarly great impacts on ecosystems, including rhinos and hippos (Owen-Smith, 1988). Herbivore species within this size range were a general feature of ecosystems worldwide until modern humans spread their predatory and land-transforming influences worldwide between 50 000 and 12 000 years ago. It has been surmised that the elimination of these megaherbivores through human hunting contributed to the demise of many other large mammal species, and consequent reduction in species diversity outside of Africa and tropical Asia, as a result of the habitat changes that occurred (Owen-Smith, 1987, 1989). This emphasises that the effects of elephants on biodiversity can be positive as well as negative. However, the biodiversity consequences need to be judged not only at the species level, but also in terms of changes in habitat composition and functional processes (Noss, 1990). This diversity is furthermore expressed across a range of organisational levels from genes to landscapes.

Formerly, ecosystem dynamics were viewed largely from a 'balance of nature' perspective, with changes being regarded as threatening the maintenance of the species richness within these systems. Hence, human interventions were largely directed at counteracting or suppressing changes, aimed at maintaining an 'ideal' state generally defined by some historical perspective, e.g. what was

described in writing by early European colonists. The modern perspective views disturbance in various forms as being integral to the generation and maintenance of biodiversity, expressed through hierarchical patch dynamics and consequent spatial heterogeneity within landscapes (Pickett & White, 1985). Hence, in this chapter we are concerned with the changes brought about through the presence of elephants on the species composition, vegetation structure and functioning of the ecosystems of which they are a component. These changes are judged within the context of the overriding context of biodiversity conservation, which is a primary aim set by humans for much of the land within which these elephants reside.

We need to distinguish further an 'elephant' effect from an 'elephant density' effect (Cowling & Kerley, 2002). The former reflects the ability of elephants to influence biodiversity, by virtue of the special characteristics of elephants, while the latter reflects the consequences that depend on the abundance of elephants within the area of concern. Bearing in mind the considerations outlined above, this chapter addresses the following specific questions.

- How are elephants special in the nature of their feeding, and hence, the damage to plants they cause, by virtue of features such as body size, the trunk and tusks?
- How are the impacts of elephants on individual plants translated into changes in vegetation composition and structure?
- How do these changes in vegetation and hence, habitat features for other animal species, affect the coexistence of these species?
- How do the presence and activities of elephants influence nutrient cycling, the effects of fire and the productive potential of the ecosystems they inhabit?
- What are the cascading or knock-on effects of elephants on the components of biodiversity?

In addition, we attempt to identify what we still need to find out in order to better understand the impacts of elephants and the implications for management of these impacts. The approach is to use these questions as a framework to guide the contents of this chapter.

Across Africa, elephants occupy a broad range of terrestrial ecosystems, penetrating deserts such as the Namib along seasonal rivers, as well as being found within the tropical rain forests of the Congo basin (Laws, 1970; Boshoff *et al.*, 2002). However, within South Africa, concern is focused on their effects

on savanna and subtropical thicket ecosystems, reflecting current elephant distribution.

SPECIAL FEATURES OF ELEPHANTS

The African elephant is the largest herbivore alive today, with females attaining a maximum body mass of over three tons and males over six tons. Coupled with this large size (and hence megaherbivore status) is a fairly simple digestive system with most digestion taking place in the capacious hindgut, comprising the small intestine and colon. Throughput is relatively rapid, with mean retention time of around 24 hours, independent of the daily food intake (Clauss *et al.*, 2007; Davis, 2007). This fast passage (compared with other large herbivores) means that digestive efficiency is quite low, with less than half of the ingested food being assimilated and the remainder passed out as faeces. On the other hand, large amounts of fibre can be ingested without slowing throughput, in contrast to the situation for ruminants (Janis, 1976). Because of their large size (hence, relatively low external surface area to volume ratio) elephants have a low metabolic rate per unit of body mass, which enables them to obtain adequate nutrition from plant material low in nutrient content. Hence, their relative daily food intake (in dry mass terms) is also low, around 1–1.5 per cent of body mass per day (compared with 2–3 per cent for cattle). Nevertheless, as a consequence of their large size, the absolute amount of vegetation that each elephant consumes per day is huge, estimated to be over 60 kg for a fully grown male, weighed as dry mass, or around 180 kg weighed wet (Owen-Smith, 1988).

FEEDING BEHAVIOUR

Elephants display a variety of feeding behaviours, and have long been known as robust and wasteful feeders (Selous, 1881). As with other vertebrate herbivores, they can ingest forage directly by biting with the mouth, although this occurs infrequently – about 10 per cent of browsing events in subtropical thicket (Lessing, 2007). Alternatively, forage is plucked (broken off the plant or the entire plant uprooted) with the trunk and passed to the mouth where it is ingested through a single bite or multiple bites, or material is stripped off a branch with the trunk and passed to the mouth. They also run branch tips between their teeth to strip off the bark, discarding the interior wood. At certain times of the year they strip off and discard leaves before consuming the bark,

while at other times they eat the leaves of these same species (Barnes, 1982; Chafota, 2007).

The trunk, a specialised foraging adaptation with surprising dexterity, plays a crucial role in enabling elephants to achieve a high rate of food intake, in part by allowing them to chew and handle material simultaneously. Food intake has been estimated to approach an instantaneous rate of $2 \text{ kg} \cdot \text{min}^{-1}$ when feeding on succulent shrubs (Lessing, 2007). The trunk, together with their high shoulder height, also allows them to forage up to 8 m above ground level (Croze, 1974). Elephants can adopt a bipedal stance in order to reach higher food material (Croze, 1974). Most browsing, however, takes place between 0.5 and 2.5 m (Guy, 1976; Jachmann & Bell, 1985; Chafota, 2007; Lessing, 2007).

The tusks are used for specialised feeding, particularly to strip bark off trees, most commonly during the latter part of the dry season and the early growing season (Barnes, 1982). Thereby elephants probably gain from the carbohydrates flowing through this bark prior to leaf flush (Barnes, 1982). When hard pressed for food, elephants will gouge quite deeply into the trunks of soft-stemmed trees like baobabs *Adansonia digitata* (figure 1). They also use the tusks to dig up the roots of some woody and succulent species (Barnes, 1982; Chafota 2007; Lessing, 2007).

Elephants use their feet to dig out (kicking or scraping) geophytes or grass tussocks, and knock grass tussocks held in the trunk against their legs to dislodge soil (Owen-Smith, 1988).

Elephants have been recorded felling or uprooting trees up to 60 cm in basal diameter (Chafota, 2007). Sometimes they feed on the branch tips or roots of these trees, but on other occasions they abandon the fallen tree without feeding on it. It has been suggested that some tree felling may be a social display unrelated to feeding (Hendrichs, 1971; Midgley *et al.*, 2005), but this has not been confirmed. Trees pushed over in Kasungu National Park, Malawi, were taller (4–5 m) for favoured species than for species generally rejected as food (2–3 m) (Jachmann & Bell, 1985).

Unlike most other herbivores, elephants' feeding actions may lead directly to the death of mature trees (through felling or uprooting), or otherwise expose these trees to other processes leading to tree mortality (through bark removal). Most other herbivores simply remove plant tissues, suppressing plant growth and reproductive potential, except in the case of small seedlings. In this sense, the consequences of elephant feeding for tree dynamics are more akin to those of a predator than is the case for other herbivores.

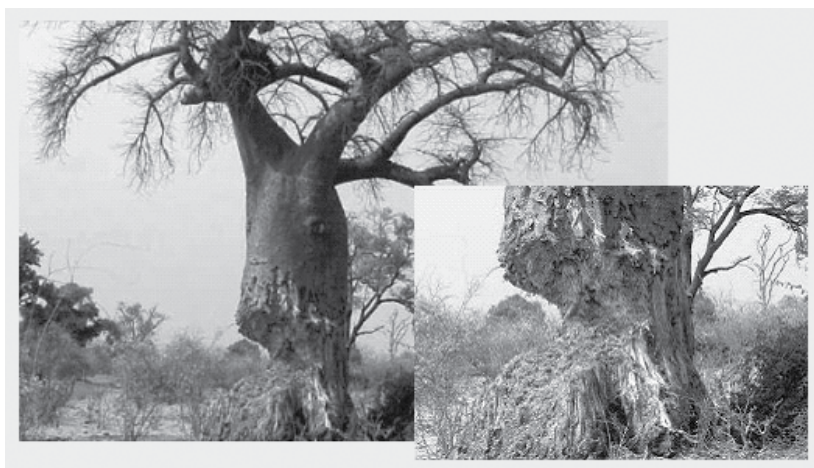


Figure 1: Damage to baobabs by elephants in the Chobe National Park, Botswana (photo: W S W Trollope)

Forage use as a basis for inferring impact

It is generally presumed that elephant herbivory is an important mechanism that structures plant communities (e.g. Laws, 1970; Tafangenyasha, 1997; Stuart-Hill, 1992; Trollope *et al.*, 1998; Mapaure & Campbell, 2002; Conybeare, 2004). Thus, it is important to have an understanding of elephant diet, and particularly their dietary preferences, in order to predict these impacts. However, some plant species that are not browsed by elephants respond to elephants through indirect mechanisms – for example, trampling and associated path formation (Plumptre, 1993; Landman *et al.*, 2008). In addition, the amount of forage ingested by elephants only represents a fraction of their total forage off-take (Guy, 1976; Paley, 1997); hence, impacts on plant communities are not a simple function of food requirements.

Although numerous studies describe the diet of elephant in a range of habitats – wooded savannas, desert shrublands, fynbos and subtropical thicket (Buss, 1961; Jarman, 1971; Barnes, 1982; Kalemera, 1989; Viljoen, 1989; Kabigumila, 1993; Paley & Kerley, 1998; Steyn & Stalmans, 2001; Milewski, 2002; Greyling, 2004; Minnie, 2006; Chafota, 2007), many are not quantitative in terms of species contribution, and for example describe diet at the broad level of growth forms (Koch *et al.*, 1995; Cerling *et al.*, 1999; Codron *et al.*, 2006). In addition, few studies (Guy, 1976; Jarman, 1971; Viljoen, 1989; De Boer *et al.*, 2000; Greyling, 2004; Minnie, 2006; Landman *et al.*, 2008) assess the relative

availability of dietary items, and are thus able to quantify preferences for specific species. Moreover, elephant diet is often indirectly inferred from plant-based studies (Penzhorn *et al.*, 1974; Barratt & Hall-Martin, 1991; Midgley & Joubert, 1991; Stuart-Hill, 1992; Moolman & Cowling, 1994; Lombard *et al.*, 2001), assuming that differences between elephant areas and areas where elephants have been excluded are the result of elephant browsing. In this regard, Landman *et al.* (2008) showed that a significant proportion of such species are not eaten by elephants.

Elephants are mixed feeders, consuming a range of plants and plant parts from grasses to browse, bark, fruit, and bulbs. Their large body size and robust feeding allow them to have a broad diet – for example, 146 plant species in subtropical thicket (Kerley & Landman, 2006). Elephant herbivory can, therefore, influence the fate of a considerable number of plant species. However, the bulk of the daily dry matter intake comes from a few species.

Elephants consume varying proportions of browse and grass depending on region, vegetation cover, water availability, soil nutrient composition, and season (Williamson, 1975; Field & Ross, 1976; Owen-Smith, 1988; Koch *et al.*, 1995; Cerling *et al.*, 1999). Grasses are primarily consumed in the rainy season (40–70 per cent of the diet), and trees or shrubs in the dry season, when grass contributes only 2–40 per cent (Buss, 1961; Bax & Sheldrick, 1963; Wing & Buss, 1970; Jarman, 1971; Field, 1971; Laws *et al.*, 1975; Williamson, 1975; Guy, 1976; Barnes, 1982; Lewis, 1986; Kabigumila, 1993; Spinage, 1994; De Boer *et al.*, 2000; Greyling, 2004). When feeding on grasses, elephants favour leaves and inflorescences during the wet season, turning more to leaf bases and roots during the dry season (Owen-Smith, 1988). Forbs (herbaceous plants besides grasses) are also commonly consumed, and elephants may spend much time feeding in reed beds during the dry season. Under dry conditions, wood, bark and roots constitute 70–80 per cent of the material eaten (Barnes, 1982).

Elephants are selective feeders at the plant species level. For example, 40–70 per cent of the seasonal browse intake of elephants feeding in the Chobe River front region of northern Botswana came from just three shrub species: *Baphia massaiensis*, *Bauhinia petersiana* and *Diplorhynchus condylocarpon*, with a wider range of species eaten during the hot-dry season than at other times of the year (Chafota, 2007). A similar pattern was observed in subtropical thicket, where 25 out of 146 species used comprise 71 per cent of the diet (Kerley & Landman, 2005). Common dietary staples elsewhere include species in the genera *Acacia*,¹ *Azima*, *Colophospermum*, *Combretum*, *Commiphora*, *Cordia*, *Cynodon*, *Dichrostachys*, *Grewia*, *Faidherbia*, *Gardenia*, *Portulacaria*, *Premna*, *Schotia*, *Sclerocarya*, *Tamarix*, *Terminalia* and *Ziziphus*. Genera rejected as food,

or eaten rarely, include *Baikiaea*, *Burkea*, *Capparis*, *Croton*, *Erythrophleum*, *Euclea*, *Ochna* and *Scolopia* (see diet references above). Several *Combretum* spp. are commonly eaten, others rejected (e.g. *Combretum mossambicense* is noted by Skarpe *et al.*, 2004).

There is conflicting evidence regarding the nutritional characteristics of plants preferred by elephants. Some studies show preferences for plants with higher levels of protein, sodium, calcium and magnesium (Dougall, 1963; Dougall & Sheldrick, 1964; Van Hoven *et al.*, 1981; Jachmann & Bell, 1985; Hiscocks, 1999), lower levels of crude fibre (Field, 1971; Holdo, 2003), secondary compounds and lignin (Jachmann, 1989). In contrast, Thompson (1975) could not show any differences in mineral or crude protein content between the bark of five species of trees with differing apparent preference. Calcium, magnesium, sodium, potassium, total salts and crude protein apparently do not determine elephant use among 16 species assessed by Anderson & Walker (1974) in Zimbabwe. These relationships are confounded by factors such as soil nutrients, rainfall, plant availability and so on, and need to be further researched.

It has been hypothesised that because of their simple digestive system, involving rapid throughput, elephants are less readily able than ruminants to handle plant secondary chemicals (e.g. resins, tannins and other phenolics), which tend to be concentrated in leaves (Olivier, 1978; Langer, 1984).

Discarded forage

Besides trees felled, elephants also break off and discard plant parts (Ishwaran, 1983). The discarded material could represent as much as a quarter to a half of the mass consumed in the Addo Elephant National Park (Addo) (Paley, 1997; Lessing, 2007). This discarded material could alter the size, distribution, nutrient levels and hence dynamics of litter in subtropical thicket ecosystems (Kerley & Landman, 2006). Elephants are not unique in this behaviour, as for example, kangaroo rats (*Dipodomys* sp.) also discard a large proportion of the forage they harvest (Kerley *et al.*, 1997). This aspect of elephant foraging is poorly described and understood, but may have profound cascading effects on ecosystem function and biodiversity patterns.

Ecological consequences of sexual dimorphism

Male elephants attain a body mass twice that of adult females (Lee & Moss, 1995), leading to differences in feeding behaviour and energetic and nutritional demands besides those associated with reproduction (Stokke & Du Toit, 2000;

Greyling, 2004; Legendijk *et al.*, 2005; Shannon *et al.*, 2006a). In addition, differences in social structure (group-living cows vs. largely solitary bulls) influence foraging (Dublin, 1996). In savanna, bulls feed more robustly on fewer plant species, but a wider range of plant parts (Stokke & Du Toit, 2000), and consume more low-quality items. Family units more frequently debark and defoliate woody plants, while bulls fell trees and dig up roots more frequently (Greyling, 2004). Males also consume a higher proportion of grass than females. The rate of tree felling by males is much greater than that of females (Guy, 1976), and males also fell substantially larger trees than females. Accordingly, the consequences of the feeding and breakage impacts of the adult male segment of the population are relatively much greater than those of family units. In contrast, in subtropical thicket, males and females show large overlaps in feeding height, pluck size and foraging rates, which do not differ between sexes (Lessing, 2007). Males, however, do access the largest biomass (branch size) per pluck, and tend to harvest more multiple stem portions per pluck (compared to the females who tend to use single stem plucks).

Furthermore, differences in habitat use between sexes have been ascribed to the differential need to access water, with breeding females being found closer to water (Stokke & Du Toit, 2002). There have, therefore, been suggestions that elephant sexes occupy different ecological niches (Stokke & Du Toit, 2000; Shannon *et al.*, 2006a) in savanna. However, Shannon *et al.* (2006b) found no sex-based habitat selection in areas where water was spatially limited.

ECOLOGICAL PROCESSES INFLUENCED BY ELEPHANTS

Elephants affect a broad variety of ecological processes through their feeding, digging and movement. For example in subtropical thicket, Kerley & Landman (2006) showed that the role of elephants (15 broad processes) was comparable to that of the balance of the vertebrate herbivore community (21 species) in terms of the number of ecological processes (table 1). In addition, by virtue of their killing, through aggressive competition, of other herbivore species such as white rhinoceros *Ceratotherium simum* and black rhinoceros *Diceros bicornis* (Slotow *et al.*, 2001; Kerley & Landman, 2006), elephants also play a role analogous to predation. The significance of elephants in all these roles, and how this differs between landscapes, has yet to be quantified. The focus on a few effects such as tree mortality may, therefore, mask both the extent and the mechanisms of elephant impacts (Landman *et al.*, 2008).

Elephant formation of 'browsing lawns', where they reduce the height of mopane veld and increase the quality of forage, is considered to be 'gardening',

analogous to the formation of 'grazing lawns' by other herbivores including snails, tortoises, geese and wildebeest (McNaughton, 1984). This shrub coppice state is advantageous for elephants through providing more food and better quality re-growth within the 2–5 m height range favoured by elephants (Jachmann & Bell, 1985). There are also increases (provided the overall cover is not lost) in the availability of forage for other herbivores (Guy, 1981; Smallie & O'Connor, 2000; Styles & Skinner, 2000; Rutina *et al.*, 2005; Makhabu *et al.*, 2006). In addition, they will excavate waterholes in dry riverbeds (Owen-Smith, 1988; Selous, 1881). The paths that they develop in travelling to and from water, and around obstacles such as mountainous ridges, can facilitate movements by other species (e.g. Skead, 2007). Elephants also function as keystone species (Paine, 1969), as shown for example by their dispersal of seeds of a specific range of plant species (Kerley & Landman, 2006). These observations appear to be consistent with the 'keystone herbivore' concept, invoked to explain how the elimination of similar megaherbivores elsewhere (through hunting by early human colonists in the late Pleistocene) contributed to a cascading sequence of extinctions among other large mammal species (Owen-Smith, 1987, 1989; Koch & Barnovsky, 2006).

EFFECTS OF ELEPHANTS ON BIODIVERSITY

If we are to understand the impacts of elephants, it is critical that the connections between elephants and the assumed impacts (defined here as changes brought about by elephants) are clearly understood and demonstrated. Elephant impacts are observed at a range of levels, from soils to coexisting mammals (reviewed below), and in all instances of such impacts, the mechanisms need to be clearly identified.

Individual plants and species

Elephants impact on plants by breaking branches/stems, stripping bark, uprooting plants and toppling trees. The persistence of plant species eaten by elephants is dependent on whether they can cope with herbivory of this nature (i.e. the relative capacity of these species to restrict, resist or compensate for the damage inflicted by resprouting and/or regrowth), or whether mortality is balanced or exceeded by recruitment and regeneration. The ability to resprout is taxon-specific: a range of species coppice readily, whereas *Aloe* spp., *Acacia goetzii*, *Acacia nigrescens*, *Acacia nilotica*, *Acacia polyacantha*, *Dalbergia melanoxylon* (Luoga *et al.*, 2004; Kruger *et al.*, 2007) and various *Commiphora*

spp. (Kruger *et al.*, 2007) have all been reported to be poor resprouters following either cutting or elephant damage.

Broad ecological process	Megaherbivores				
	Elephant	Black rhinoceros & hippopotamus	Meso-herbivores	Omnivores	Carnivores
No. of species in category	1	2	19	3	18
Trophic processes					
Bulk grazing	1	1	3		
Concentrate grazing	1		9		
Browsing	1	1	7	3	
Frugivory	1	1	17	3	6
Predation				2	18
Scavenging				2	9
Transport processes					
Seed dispersal	1	2	19	3	6
Nutrient dispersal	1	2	19	3	18
Habitat architecture processes					
Plant form	1	2	7		
Grazing lawns		1	5		
Path opening	1	2	5	1	
Bipedurbation processes					
Wallowing formation	1	1	1	1	
Soil movement through dust bathing	1		5		
Digging	1		1	2	6
Hoof action	1		19	1	
Geophagy	1				1
River-bed configuration	1	1			
Other processes					
Litter production	1	1		2	
Germination facilitation	1	2	19	2	6
Total no. of processes affected	15	12	14	12	8

Table 1: The relative role of elephants in broad ecological processes ($n = 19$), modified from Kerley & Landman (2006), operating in subtropical thicket in relation to other megaherbivores (2 spp.), mesoherbivores (19 spp.), omnivores (3 spp.) and carnivores (18 spp.)

Responses to bark stripping also vary across taxa, e.g. *Acacia xanthophloea* in Amboseli, Kenya, are relatively tolerant of bark stripping and branch removal by elephants (Young & Lindsay, 1988). *Brachystegia* spp. seem to be highly susceptible to elephant damage, despite their high coppicing ability, resulting in stands of tall trees being converted to shrubby coppice regrowth (Thompson, 1975; Guy, 1989). O'Connor *et al.* (2007) suggest that the sensitivity of woody species to elephant browsing is a function of plant and landscape features.

Through their feeding, elephants can 'negatively' impact plant species and cause extirpation (localised plant species extinction) (Penzhorn *et al.*, 1974; Western, 1989; O'Connor *et al.*, 2007) or conversely, trigger plant growth and regeneration (Stuart-Hill, 1992).

Mechanisms of impact on individual plants

Toppling effects

The ecological effects of pollarding (total breaking of the stem) differ from toppling, where the roots may be removed from the soil, which usually kills the plant. However, if the roots remain in the soil, many species can resprout quite effectively (e.g. *Combretum apiculatum* – Eckhardt *et al.*, 2000). Factors that influence vulnerability to being toppled include strength of the wood, the depth and extensiveness of the root system and substrate stability (O'Connor *et al.*, 2007). Shallow-rooted shrubs (e.g. *Commiphora* spp.) that are uprooted completely by elephants are greatly reduced in their prevalence by elephants, as has happened in sections of Tsavo East National Park, Kenya (Leuthold, 1977), and in Ruaha National Park, Tanzania (Barnes, 1985).

Bark stripping

The impact of stripping on a plant species is dependent on the degree to which the bark is stripped. Ring barking will kill the plant, but if some phloem remains intact, the bark may re-grow (Buechner & Dawkins, 1961; Laws *et al.*, 1975). This may vary between species – mopane can lose up to 95 per cent of the bark without visible signs of stress (Styles, 1993). Features of the tree influence its vulnerability to being stripped, for example, elephants can cause more damage to trees with stringy bark (e.g. *Acacia* spp.) than those with bark that breaks off in chunks (e.g. *Sclerocarya birrea*) (O'Connor *et al.*, 2007). Furthermore, toxins in the bark or stem spinescence reduce preference for bark stripping (Sheil & Salim, 2004; Morgan, 2007). Fluted or multistemmed trunks are better protected against stripping (Sheil & Salim, 2004): in *Balanites*

maughamii two-thirds of the bark is protected on account of fluting; while multistemmed trees that avoid total stripping (O'Connor *et al.*, 2007) include various *Combretum* and *Gymnosporia* spp. Further, Sheil & Salim (2004) found that elephants selectively stripped larger trees.

The effects of stripping are exacerbated by borer infestation, rot and fire (Laws *et al.*, 1975; Thompson, 1975). Elephant bark stripping facilitates insect and fungal attacks in *Brachystegia boehmii* woodlands in northern Zimbabwe (Thompson, 1975). However, Smith & Shah-Smith (1999) found no relationship between elephant damage and fungal infection. Van Wilgen *et al.* (2003) suggest that it is highly likely that fire in conjunction with elephant impacts may have resulted in the loss of large trees in Kruger between 1960 and 1989 (see Eckhardt *et al.*, 2000).

Vulnerability of seedlings

Few studies explore elephant impact on seedlings (but see Jachmann & Bell, 1985; Kabigumila, 1993; Barnes, 2001), though there is evidence for species-specific impacts. Examples are baobabs (Edkins *et al.*, 2007), and about 35 per cent mortality in *Acacia erioloba* in Chobe National Park, Botswana (Barnes, 2001). Elephants cause mortality by ripping seedlings from the soil, or prevent recruitment into adult size classes through top kill, maintaining the plants in a size class where they are caught in the 'fire trap' (Barnes, 2001).

Case studies of species-specific impacts

Baobab *Adansonia digitata*

Elephants are the only herbivores that can kill adult baobabs, and are frequently linked to the reduction in baobab densities, e.g. Mana Pools (Swanepoel, 1993), Tanzania (Barnes *et al.*, 1994) and Kruger (Whyte *et al.*, 1996). Barnes *et al.* (1994), in a 10-year study in Tanzania, found that baobab populations declined as elephant numbers increased and that the baobabs recovered when elephant populations declined due to poaching.

As with other species, the impact of elephants on baobabs is confounded by interactions with drought (Whyte *et al.*, 1996), other herbivores (Edkins *et al.*, 2007), and fire. Furthermore, the pattern of elephant effects on baobabs is inconsistent across size-classes, either showing selection against small trees (Weyerhaeuser, 1985; Barnes, 1985), or no size-class selection (Swanepoel, 1993).

Spatial refuges for baobabs occur on steep slopes inaccessible to elephants (figure 2; Edkins *et al.*, 2007). Consequently, it is unlikely that elephants can remove all baobabs from areas that include sufficient topographic relief (Whyte *et al.*, 1996; Edkins *et al.*, 2007).

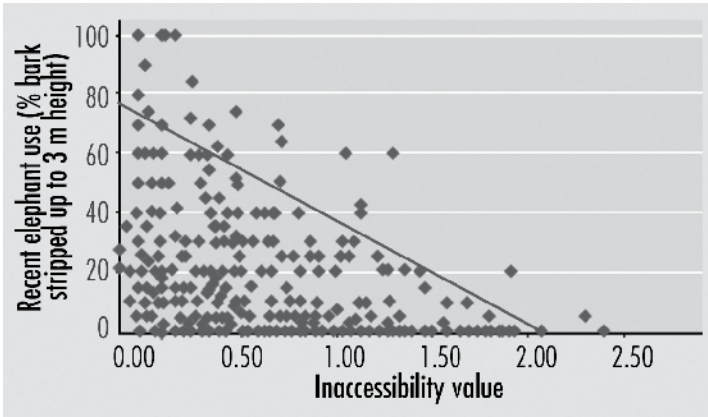


Figure 2: Regression analysis at the 90th quantile of recent elephant use of baobabs in the Kruger National Park and the inaccessibility value calculated for these. Elephant browsing drops below 100 per cent at the 7° slope and below 20 per cent at the 18° slope cut-off (Edkins *et al.*, 2007)

***Acacia* spp.**

Because *Acacia* spp. are commonly selected by elephants (Calenge *et al.*, 2002), and show little or no resprouting once mature, their densities decline under high elephant browsing pressure, e.g. *Acacia tortilis*, *A. xanthophloea*, *A. nigrescens*, *A. senegal* or *A. erioloba* (Van Wyk & Fairall, 1969; Pellew, 1983; Ruess & Halter, 1990; Barnes, 2001). However, *Acacia* spp. have the capacity to regenerate rapidly from seedlings (Western & Maitumo, 2004), and elephants tend to ignore early stage and regenerating trees (Okula & Sise, 1986; Mwalyosi, 1987, 1990; Pellew, 1983; Calenge *et al.*, 2002). Thus, elephant damage may not affect *Acacia* populations overall (Balfour, 2005). In a comparative study of eight co-occurring *Acacia* spp. in Hluhluwe-Umfolozi Park, while levels of impact varied between the different species, no species were selected for or against (Balfour, 2005). In contrast, Western & Maitumo (2004) showed that elephants have brought about the local loss of swamp-edge *A. xanthophloea* woodlands in Amboseli, Kenya, their impacts overriding those of fire or other processes.

Soil chemistry confounds the latter results, however, as rising salinity levels were clearly linked to *A. xanthophloea* mortality in non-swamp areas in both Amboseli, Kenya (Western & Van Praet, 1973), and Ngorongoro, Tanzania (Mills, 2006).

Marula *Sclerocarya birrea*

Despite concern about the impacts of elephants on marula, early studies (Coetzee *et al.*, 1979), suggested that these impacts did not constitute a threat. Gadd (2002) showed that elephant impacts on marula are sustainable (low mortality rates, recovery of affected trees, no selection for small trees) in three populations adjacent to Kruger. However, other studies have shown that marula trees have suffered severe attrition due to elephants (e.g. Weaver, 1995). In Kruger, Jacobs & Biggs (2002) showed a 7 per cent mortality of marula trees, mostly ascribed to the breakage of main stems by elephants. They also showed that these impacts varied in terms of the extent (number of trees affected) and severity (amount of damage to a tree) across landscape types. Jacobs & Biggs (2002) also highlighted the concern that elephant damage could lead to increased mortality due to other factors such as insect or pathogen attack and fire.

Mopane *Colophospermum mopane*

Elephants browse intensively on mopane trees, and prefer mopane to many other trees (Ben-Shahar, 1993). However, mopane trees are well adapted to regenerate after elephant browsing, and few are killed by this browsing. While unbrowsed mopane has treelike morphologies, mopane woodlands may be converted to stands of shrubby coppice through the feeding impacts of elephants (Lewis, 1991; Smallie & O'Connor, 2000; Styles & Skinner, 2000; Legendijk *et al.*, 2005). Elephants inhibit height recruitment by repeatedly breaking leader shoots (Anderson & Walker, 1974). However, elephants have more impact in taller mopane, where ring-barking, heavy browsing and toppling cause mortality (Caughley, 1976a; Lewis, 1991).

Several factors affect the degree of elephant damage on mopane. Proximity to water sources appears, as in many other systems, to have the greatest effect (Styles & Skinner, 2000). Soil type also appears important: soils that promote shrub-like mopane yield less stable woodlands than soils that promote tree-like growth (Lewis, 1991). Elephant browsing intensity also tends to fluctuate with time of year, being greatest after spring rains (Styles & Skinner, 2000).

Spekboom *Portulacaria afra*

Spekboom is generally one of the most abundant species in subtropical thicket, and probably the best studied example of the species-specific impacts of elephants in Addo. The roots, shoots and leaves are utilised extensively (contributing about 9 per cent to the diet), usually in proportion to availability (Landman *et al.*, 2008). Elephants reduce the height of individual plants (Stuart-Hill, 1992) and remove more than 50 per cent of the biomass (Penzhorn *et al.*, 1974). Despite these high levels of utilisation (and thus large impacts), *P. afra* persists in the presence of elephants, except in areas with extremely high elephant densities (Barratt & Hall-Martin, 1991). Stuart-Hill (1992) argued that the species is adapted to the 'top-down' browsing by elephants, whereby the lower rooted branches escape elephant browsing impacts, which facilitates vegetative reproduction. The 'top-down' hypothesis is supported by observed elephant browsing heights of above 50 cm in Addo. However, this hypothesis fails when the plants are uprooted and the roots are consumed (Stuart-Hill, 1992; Lessing, 2007).

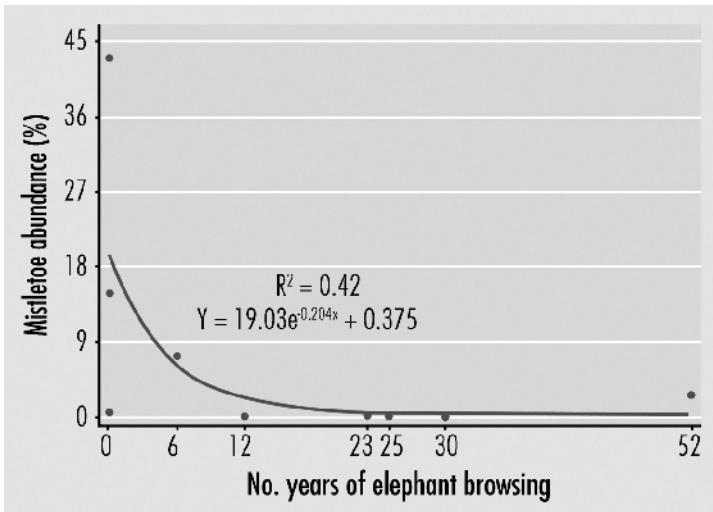


Figure 3: Exponential decline in the abundance of mistletoes (*Viscum rotundifolium*, *Viscum crassulae*, *Viscum obscurum*) in the presence of elephants in the Addo Elephant National Park (Magobiyane, 2006)

Mistletoes

Mistletoes (comprising *Viscum rotundifolium*, *Viscum crassulae*, *Viscum obscurum*, *Moquinella rubra*) are highly nutritious (Midgley & Joubert, 1991) and are preferred food items for elephants in Addo (Landman *et al.*, 2008). This guild is treated as an entity here. Mistletoes show an exponential decline in abundance (figure 3) and richness with increasing levels of elephant browsing, with *V. crassulae* disappearing in the presence of elephants (Magobiyane, 2006). *V. rotundifolium*, however, persists at very low densities in elephant habitat. These responses are rapid (a 60 per cent decline in abundance within six years), and after a decade of elephant browsing, mistletoe densities are too low to be used as measures of elephant impact (Magobiyane, 2006).

***Aloe* spp.**

Aloes, in particular *A. africana*, have long been known to disappear from the elephant area of Addo, presumably as a result of elephant browsing (Penzhorn *et al.*, 1974; Barratt & Hall-Martin, 1991). Only recently did Landman *et al.* (2008) show that elephants actually consume *A. africana*, albeit in very small proportions (about 0.1 per cent of the diet). Aloes appear to be particularly sensitive to the impacts of elephants (relative to *P. afra* and mistletoes) and disappear rapidly at very low levels of herbivory. This suggests that alternative mechanisms of elephant impact, such as trampling, may be responsible for the disappearance of the species (Landman *et al.*, 2008).

Assessing species-specific vulnerability

The above examples show that plants respond differently to elephant use. Some species decline rapidly, while others are able to persist in the presence of elephants, albeit with altered growth forms. These responses are, however, difficult to interpret due to the presence of a range of confounding variables such as fire, soil nutrients, other herbivores, and elephant densities. O'Connor *et al.* (2007) provide a theoretical framework for assessing the vulnerability of a plant species to extirpation/extinction. They list a range of plant traits, landscape characteristics that might influence the probability of elephants' selection for these species, and management unit characteristics that exacerbate these.

Plant traits

A species would be considered vulnerable to extirpation by elephants if it displayed the following characteristics:

- lacks the ability to sprout as adult and/or cannot regrow its bark so that pollarding or ringbarking causes death
- restricted to selected foraging habitats
- highly selected by elephants
- frequently subjected to pollarding and ringbarking
- regenerates infrequently and/or usually in small numbers
- slow growing
- displays episodic recruitment.

Landscape and management unit characteristics

Vulnerability to extirpation is exacerbated if:

- terrain lacks topographical refuges
- there are no spatial refuges from elephant because distance from water is not a foraging constraint
- reserves are small
- reserve is located in a semi-arid region with variable grass production, hence heightened utilisation of woody material
- reserve is a degraded semi-arid savanna in which suitable grass is no longer available and woody plants form the bulk of the diet.

Fauna

The direct effects of elephants on other animals include direct mortalities and interference competition (as opposed to resource competition). Thus, elephants temporally exclude other species from resources such as waterholes or other resources by actively chasing them away (Owen-Smith, 1996). Alternatively, elephants may also facilitate access to resources through, for example, excavating waterholes (Owen-Smith, 1988) and increasing the availability and quantity of forage (e.g. Skarpe *et al.*, 2004). The understanding of these interactions is again limited due to confounding factors, and the fact that these are normally cascading effects.

Invertebrates

There are few studies on the effects of elephants on invertebrates. Cumming *et al.* (1997) found significantly lower richness of ant species in woodlands that had been impacted by elephants than in intact woodlands. Cicadas were only recorded in the intact woodlands, not in the impacted woodlands.

Mantid communities did not respond to changes in woodland structure (Cumming *et al.*, 1997).

Dung beetles are sensitive to habitat change (Klein, 1989). Disturbance in the form of fire or elephants can have a significant effect on dung beetle species' diversity and biomass (Botes *et al.*, 2006). In Tembe Elephant Park, Maputaland, dung beetle assemblages (Botes *et al.*, 2006) differ between elephant impacted sand forest (a key endemic habitat type) and undisturbed sand forest sites (including the loss of some forest specialist species). Elephants may provide refugia for other species, particularly ground-living invertebrates, under dung and trunks of toppled trees (Govender, 2005).

Musgrave & Compton (1997) demonstrated a significant increase in phytophagous insect feeding damage in the presence of elephants in Addo, and attributed this to an increase in the quality of browsed plants through a decline in secondary chemical compounds (e.g. tannins). This hypothesis has yet to be tested, nor has it been shown which insect species were involved, and what their population or overall insect biodiversity responses were. This apparent increase in nutritional quality of plants needs to be weighed up against the significant decline in overall plant phytomass (Kerley & Landman, 2006).

Reptiles and amphibians

In an attempt to explain high tortoise abundance in Addo, Kerley *et al.* (1999) hypothesise that elephant alteration of subtropical thicket habitat (through their creation of open habitat patches and paths) may favour increased access for tortoises (i.e. leopard tortoises *Stigmochelis pardalis* and angulate tortoises *Chersina angulata*).

Birds

Cummings *et al.* (1997) found a drop in species richness of birds and changes in bird communities (from woodland species to non-woodland species) in response to changes caused by elephants in Miombo woodlands, Zimbabwe. Reduced vertical and horizontal heterogeneity in the elephant-impacted woodlands probably accounts for their observed loss of species richness (c.f. MacArthur, 1964).

In contrast, Herremans (1995), assessing bird community species shifts in riverine forest and Mopane woodland in northern Botswana, found that dramatic woodland change associated with the high abundance of elephants did not result in a reduction in bird diversity. This was possibly due to the fact

that woodland conversion was spatially restricted. However, gallinaceous birds were more abundant in areas heavily impacted by elephants than elsewhere in the Chobe River region (Motsumi, 2002).

Elephant removal of large standing trees in savanna (e.g. Eckhardt *et al.*, 2000), may decrease the availability of nesting sites for raptors, especially vultures and other rare, open-savanna species (Monajem & Garcelon, 2005). Little is available in the scientific literature on the nesting requirements of savanna raptors. More research is needed to determine the outcomes of elephant-raptor interactions.

Chabie (1999) showed that in transformed thicket in Addo, there were significant changes in the bird communities. At the guild level, there was a shift from frugivores in intact thicket to a community dominated by insectivores and granivores in opened-up thicket. In addition, there was a shift to larger bodied species in transformed thicket. The hypothesis that elephants drive these changes needs to be further tested.

Bats

The expected loss of large trees and snags due to elephants may decrease both roosting sites of bats and available habitat for species that specialise on feeding within dense vegetation (Fenton *et al.*, 1998). However, Fenton *et al.* (1998) found no decrease in Vespertilionid and Molossid (airborne insectivores) bat species richness, or a loss in specialists, with a reduction in woodland canopy cover. Similar results were observed by Cumming *et al.* (1997) in Miombo woodlands.

Small terrestrial mammals

There are few studies on the impacts of elephants on small mammals. Keesing (2000) showed that the presence of elephants in East African savannas results in an increase in species richness of small mammals, through habitat alteration.

Large terrestrial mammals

Browsers

There is a general negative correlation between elephant biomass and the biomass of browsers and medium-sized mixed feeders across ecosystems (Fritz *et al.*, 2002). A number of mechanisms for this have been proposed, including

(1) the reduction in resources through direct competition, (2) the alteration of habitats for browsers and other ungulates, (3) increase in visibility resulting in higher predation levels, and (4) competition for water (Owen-Smith, 1988; Skarpe *et al.*, 2004; Valeix *et al.*, 2007). While the patterns are significant, and sometimes obvious, the mechanisms are not yet clear: a possible explanation is that elephants reach highest abundances in areas of mopane and other vegetation types which they exploit more effectively than other browsers.

The structural transformation from more wooded to more open habitat conditions benefits some browser species, but leads to a decline in others. The persistent abundance of elephants along the Chobe River and in Hwange National Park has been associated with an increase in kudu *Tragelaphus strepsiceros* and impala *Aepyceros melampus* (Skarpe *et al.*, 2004). The mechanism for this is not clear, however; on the Chobe River, it may reflect the increase in *Capparis tomentosa* vines and *C. mossambicensis* shrubs, which are readily consumed by kudu and impala, but not elephants. In contrast, along the Chobe River, the abundance of bushbuck *Tragelaphus scriptus* has declined substantially following the opening of the riparian woodland by elephants (Addy, 1993).

In Addo, the opening of the succulent thicket vegetation by elephants brought about a decline in bushpig *Potamochoerus larvatus*, Cape grysbok *Raphicerus melanotis* and bushbuck abundance (Novellie *et al.*, 1996; Castley & Knight, 1997). However, it is not known whether populations of these species outside the elephant enclosure have remained unchanged over this period, or whether putative changes in habitat structure are the consequences of elephant impacts (reasonably likely given the trends reviewed here) or some other process such as global climate change (Kerley & Landman, 2006).

The reduction of vegetation cover and density by elephants in Addo results in a change in potential browse availability for black rhinoceros (Kerley & Landman, 2006). The increase in elephant paths, associated with increases in elephant densities, initially facilitates access to browse by black rhinoceros, but the subsequent dominance of the landscape by these paths results in a loss of foraging opportunities.

Sigwela (1999) compared the diet of kudu in the elephant enclosure and botanical reserves of Addo, and showed that elephants had no apparent effect on kudu diet selection. This is surprising given that (1) extensive vegetation changes have occurred in the elephant enclosure, (2) kudu diet (28 species) includes many of the plant species recorded as being impacted by elephants, and (3) elephants consume all the plant species recorded in the diet of kudu here. This suggests that food availability is not limiting to either kudu or elephant

at the present densities of vegetation and browsers at these sites (Kerley & Landman, 2006).

Grazers

Given that grass forms a substantial part of the diet of elephants for much of the year (Owen-Smith, 1988), elephants are expected to compete with grazing ungulates if forage is limited. On the other hand, elephants are able to open up the woodland and increase the grass cover (Caughley, 1976b). However, in their broad-scale analysis, Fritz *et al.* (2002) could not detect any effect of elephants on grazers. Western (1989) highlighted the role of elephants in East Africa in facilitating pasture for medium and small ungulates, including domestic livestock.

In several cases, the decline of grazing species has been linked to the encroachment of woody vegetation in the absence of elephants (Owen-Smith, 1988), for example wildebeest *Connochaetus taurinus*, plains zebra *Equus burchelli*, waterbuck *Kobus ellipsiprymnus*, and reedbuck *Redunca arundinum* in Hluhluwe-Umfolozi Park (Owen-Smith, 1989). In Tsavo East National Park, Parker (1982) reported an increase in abundance of several grazing species, including oryx *Oryx gazella*, warthog *Phacochoerus africanus*, and zebra, following the opening of shrubland by the increasing elephant population. Young *et al.* (2004) found that by decreasing cattle grazing in a grassland area, elephants reduced the effects of competition between livestock and zebra.

Not all grazers benefit; for example, the conversion of tall woodlands into shrub coppice is likely to be adverse for sable antelope *Hippotragus niger*, although possibly not for roan antelope *Hippotragus equinus* (Bell, 1981).

Buffalo *Syncerus caffer* show a variety of responses to elephants. In the Chobe region, buffalo herds favoured areas recently grazed by elephants, suggesting facilitation rather than competition (Halley *et al.*, 2003). Skarpe *et al.* (2004) suggested that there is no evidence for competition between buffalo and elephants in Chobe; however there is some evidence for competition between buffalo and elephants in Tanzania (De Boer & Prins, 1990).

Ecosystem patterns and processes

The population and species level impacts brought about by elephants (documented in part above) will be expressed at the community and ecosystem level, including emergent properties of such systems, such as nutrient cycling, vegetation structure and dynamics.

Nutrient cycling

Elephants typically constitute 30–60 per cent of the large herbivore biomass in savanna ecosystems, and are thus responsible for 25–50 per cent (allowing for metabolic scaling) of the plant biomass consumption by herbivores (Owen-Smith, 1988; Fritz *et al.*, 2002). About 50 per cent of the material eaten passes through the gut undigested. Furthermore, elephants process fibrous plant parts such as bark and roots (which are generally not eaten by other herbivores) and thereby accelerate biomass recycling. Their importance for biomass cycling is further enhanced through wasteful feeding (Paley, 1997; Lessing, 2007) and the toppling of trees (Owen-Smith, 1988).

This contribution by elephants to biomass recycling tends to be greater in nutrient-poor than in nutrient-rich ecosystems because of their capacity to exploit vegetation components of low nutritional value. The removal of branch ends as well as leaves, plus felling of mature trees, promotes compensatory regeneration by these plants (Pellew, 1983; Fornara & Du Toit, 2007; Makhabu *et al.*, 2006) and, hence, greater primary production and rates of nutrient recycling than would occur in the absence of elephants. Termites contribute to the release of the nutrients in the fibrous tissues in elephant dung, and fire to releasing the minerals held in the stems of trees toppled by elephants. It has been hypothesised that, in the nutrient-deficient savanna woodlands prevalent on Kalahari sands (with little capacity to retain nutrients), much of the biologically available nitrogen and sodium pool is held within elephant biomass (Botkin *et al.*, 1981).

Elephants play a variety of roles in nutrient cycling, especially in nutrient-deficient ecosystems. They may release the nutrients locked up in tree trunks and roots (Botkin *et al.*, 1981). By removing large trees, they reduce the role that these trees play in extracting mineral nutrients from deep soil layers (Treydte *et al.*, 2007), and also the contribution of these trees to small-scale heterogeneity in soil nutrients through the nitrogen-enrichment promoted by fallen leaves. This generally decreases the availability of high-quality forage resources beneath tree canopies, and could indirectly affect the persistence of grazers (Ludwig, 2001). By reducing the prevalence of nitrogen-fixing legumes such as many *Acacia* spp., elephants suppress the role that these species play in nitrogen enrichment (Treydte *et al.*, 2007), although the absolute and relative extent of this effect has not been quantified.

Soil resources

Because of their large biomass, the trampling effects of elephants on soil compaction can also be substantial, with unclear consequences for vegetation (Plumptre, 1993). The large increase in woody cover associated with the exclusion of elephants in the experimental plots in Uganda dramatically increased soil organic matter and thereby pH, as well as extractable calcium, potassium, and magnesium levels. Organic carbon and nitrogen also increased, but total phosphorus declined slightly (Hatton & Smart, 1984).

Kerley *et al.* (1999) showed that in the Addo elephant enclosure the proportion of the landscape that represented run-on zones (i.e. where resources such as water, litter, soil, and nutrients are trapped during overland flow) declined, while the proportion of run-off zones (i.e. where these resources are lost) increased. The consequence of this was a decline in soil nutrients. Kerley *et al.* (1999) suggested that elephant impacts were less deleterious than goat impacts, but that these studies must be replicated.

Seed dispersal

Elephants play an important role in facilitating the dispersal and germination, and hence regeneration, of a large variety of plant species through endozoochory. Elephants are considered to be the only foragers (and hence dispersers) of the large-fruited *Balanites wilsoniana*, a canopy tree dominant in Kibale Forest, Uganda, as well as other large-fruited forest species (Chapman *et al.*, 1992; Babweteera *et al.*, 2007). Elephants enhance seedling germination (Cochrane, 2003) and increase seedling survival and growth by dispersing propagules far from adult trees (Babweteera *et al.*, 2007). In savanna, seed germination and seedling survival of *Sclerocarya birrea* are also enhanced following fruit ingestion by elephants (Lewis, 1987).

Despite their dietary breadth in subtropical thicket (146 plant species – Kerley & Landman, 2006), elephants are relatively poor seed dispersers in Addo, dispersing only 21 plant species through endozoochory (Mendelson, 1999; Sigwela, 2004), comparable to black rhinoceros and eland (both 20 species – Mendelson, 1999). Why so few species are dispersed is not clear, but may reflect the rarity of most plant species in the diet (25 out of 146 species comprise 71 per cent of the diet – Kerley & Landman, 2005), selective foraging behaviour in terms of plant phenology, complete loss of propagules during digestion, or inadequate sampling. The large volume of forage intake (and faecal output) by elephants (Owen-Smith, 1988), however, allows them to disperse large numbers

of seeds (Sigwela, 2004), but their role in plant regeneration through this process needs to be quantified. Levels of zoochory vary between locations: for example, Robertson (1995) recorded 32 dicotyledonous species that were dispersed by elephants in nearby Shamwari Private Game Reserve.

Mortality of seeds during passage through the digestive tract was significantly lower in elephant compared to the goat *Capra hircus*, which served as a model ruminant (Davis, 2007). The effects of passage through the elephant digestive tract on germination differed between plant species (e.g. *Acacia karroo* germination declined, while *Azima tetracantha* germination improved). In addition, patterns of germination after ingestion differed between elephants, goats and pigs (Davis, 2007). This suggests that elephant effects on endozoochory will not be replaced by other herbivores.

Comparison among ecosystems

Perceptions of the extreme vegetation transformation that can be brought about by burgeoning elephant populations have been strongly influenced by particular case studies from outside South Africa. These include the situations in Murchison Falls National Park, Uganda, which led to the first major elephant culling operation implemented in Africa; Tsavo East National Park, Kenya, where a need for drastic culling was proposed but not implemented in the face of opposition; and Chobe National Park, Botswana, where high elephant concentrations have developed in the vicinity of the Chobe River, and culling has been repeatedly advocated but not undertaken because of practical considerations. Most recently, drastic vegetation changes ascribed to elephants have been documented for Amboseli National Park, Kenya. A critical appraisal of the ecological context and what these particular examples show (or do not show) is helpful, before turning to a broader assessment of ecosystem differences.

Illustrative case studies

Murchison Falls in Uganda

Murchison Falls National Park covers a 2 400 km² section of the northern part of the Bunyoro district in western Uganda, divided into southern and northern sections by the Nile River. Elephants were spread more widely over a 3 200 km² range at the time of the study (Laws & Parker, 1968; Laws *et al.*, 1975). The annual rainfall of 1 250 mm supported a *Terminalia glaucescens/Combretum binderanum* savanna woodland, plus open grassland areas with scattered

Acacia sieberiana trees. Also present were patches of closed-canopy forest (including the Budongo Forest), which historically had been more widespread, plus a limited area of bushland. Soils are underlain by basement igneous rocks, with volcanic influences from the adjoining Rift Valley. Annual burns generally occurred early in the dry season. A population approaching 10 000 elephants had become compressed inside the park by surrounding human settlements, creating an effective regional elephant density of around 3 elephant.km⁻². The park also supported 6 000 hippos and 14 000 buffaloes, plus numerous kob *Kobus kob*, hartebeest *Alcelaphus buselaphus* and warthog, so that the total large herbivore biomass amounted to 12 000 kg.km⁻². Much of the central region had been transformed into treeless *Hyparrhenia* grassland with just tree stumps remaining.

Vegetation changes were documented from aerial photographs (Laws & Parker, 1968; Laws *et al.*, 1975). One section of woodland, covering 5 300 km² in 1958, in which 24 per cent of trees were dead (Buechner & Dawkins, 1961), had been reduced to 1 060 km² in 1967, with 98 per cent of trees dead. The radial pattern of damage diminishing outwards from the centre of the park indicated that fire was not the major cause of the tree mortality. In some areas woodland had been replaced by dense *Lonchocarpus taxiflorus* shrubland, apparently resistant to both heavy browsing and fire. Two exclosures established in 1967 had become transformed to closed canopy *A. sieberiana* woodland, 7–10 m high by 1981 (Smart *et al.*, 1985). However, plant species richness had dropped to almost half of that recorded in 1967, especially in the herbaceous layer. Following the build-up of soil organic matter, there was a dramatic increase in extractable cations associated with an elevated soil pH (Hatton & Smart, 1984). Although total soil phosphorus declined, available phosphorus and nitrogen both showed increases. Following a massive reduction of the elephant population during the 1978 civil war, abundant regeneration of dense *Acacia* scrub occurred through much of the formerly open grassland areas of the park and extended into formerly *Terminalia* woodland. However, fire frequency was also reduced during this period.

A point to note in this case history is evidence that elephant damage was the primary factor, and fire secondary in the woodland transformations that occurred. It is also noteworthy that floristic diversity was reduced when elephants were excluded, at least in the herbaceous layer. Furthermore, tree regeneration took place rapidly when elephant impacts were reduced, although not back towards the former woodland composition.

Tsavo in Kenya

Tsavo East and West National Parks cover a combined area exceeding 20 000 km² in south-eastern Kenya, divided by the Mombassa road and railway line. Annual rainfall averages around 400 mm in central Tsavo East. Here, the vegetation consists predominantly of *Commiphora* shrubland on acid alluvial soils, with bands of tall trees and other species flanking rivers. Woodland decline had become a source of concern by 1967, at which stage the elephant population had reached at least 24 000 animals (Glover, 1963; Agnew, 1968). Severe drought conditions with rainfall amounting to less than half of the long-term mean prevailed during 1971, resulting in the deaths of at least 7 000 elephants (Corfield, 1973), representing 15–20 per cent of the pre-drought population (Cobb, 1976). *A. tortilis* plants taller than 1 m declined in density by 65 per cent between 1970 and 1974, while baobab trees had been virtually eliminated by 1974 (Leuthold, 1977). Mature *Commiphora* shrubs were reduced in density from 90 plants.ha⁻¹ in 1970, to 5 plants.ha⁻¹ by 1974 in a 4 400 km² section of Tsavo East (the rest of the park showed far less change – Myers, 1973). The opening of the woodland, promoted further by fires, led to increases in the abundance of grazers such as Burchell's zebra and oryx, while browsers including lesser kudu *Tragelaphus buxtoni*, gerenuk *Litocranius walleri* and giraffe *Giraffa camelopardalis* declined (Parker, 1982). Black rhino numbers also fell drastically, with poaching responsible for most of the losses.

Poachers also reduced the elephant population within the park to around 6 000 animals by 1994. This lowered density, then allowed abundant woodland regeneration to occur, especially of *A. tortilis* in riparian fringes (Van Wijngaarden, 1985; Leuthold, 1996). *Commiphora* shrubs that had been pushed over resprouted profusely from the base of the stem or roots. Some tree species not eaten by elephants survived virtually unchanged from 1970. Associated with the recovery of woody vegetation, the abundance of lesser kudu and gerenuk increased while the grazers that had shown increases decreased in numbers (Inamdar, 1996).

The Tsavo case illustrates drastic vegetation transformation by elephants during a severe drought followed by the rapid recovery of this vegetation after the abundance of elephants had been reduced to a density of around 0.3 animals.km⁻². These changes occurred mostly in the more arid region of the park. Populations of other large herbivores were affected to a relatively minor extent. Hence, no biodiversity losses occurred, apart from the near-extirpation of baobab trees (which occur abundantly outside the park). The major uncertainty is what would have happened had the peak density level of around 2 animals.km⁻² been maintained for longer.

Chobe River front and adjoining areas in northern Botswana

The 80 000 km² region of northern Botswana within which Chobe National Park lies supported an elephant population which had reached 40 000 animals in 1980 and 140 000 animals by 2006 (Spinage, 1990; Skarpe *et al.*, 2004). Recent dry season densities along the Chobe River front region average around 4 elephants.km⁻², decreasing to 0.5 elephants.km⁻² when these animals disperse during the wet season (rainfall is around 700 mm per year). A narrow strip of riparian forest persisted along the Chobe River front in 1970, although many of the large *Acacia* trees appeared to be dying (Simpson, 1975). By 1980 most trees near the river, mainly *A. nigrescens* and *A. tortilis*, had been reduced to standing dead trunks, while two species unpalatable to elephants (i.e. *Combretum tomentosum*, *C. mossambicense*) had become predominant in the shrub understorey. Further back from the river, a shrubland including *C. eleagnoides*, *Baphia massaiensis* and *Bauhinia petersiana* prevailed on the alluvial terrace, while 3–5 km away from the river the vegetation changed to sandveld woodland with *Burkea africana* predominant on shallower sandy soils and *Baikiaea plurijuga* on deeper sands. Aerial photographs indicated that the area covered by woodland decreased from 60 per cent to 30 per cent between 1962 and 1998, while the area of shrubland expanded from 5 per cent to 33 per cent (Mosugelo *et al.*, 2002). In 1874, before elephants were exterminated from the region by ivory hunters, the vegetation adjoining the Chobe River had appeared quite open (Selous, 1881). Vegetation on the alluvial terrace remained open through the 1930s, with grazing by cattle plus exclusion of fires before the national park was established, contributing to the thicket development (Simpson, 1978).

A study on the ecosystem consequences of these vegetation changes (Skarpe *et al.*, 2004) found little regeneration of the tree species reduced in abundance by elephants, largely due to intense browsing pressure on seedlings by a high density of impala (locally >150 animals km⁻²). The shrub species avoided by elephants were commonly browsed by ruminants (Makhabu *et al.*, 2006), while buffalo appeared to be more abundant in areas of the floodplain where elephants had been feeding than elsewhere. Both small mammals and gallinaceous birds (guinea fowl and spur fowl) appeared more abundant in places that had incurred severe elephant impacts. The Chobe River front retained an exceptionally high density of land birds, especially of migrants (Herremans, 1995). Nevertheless, the opening of the woody vegetation cover by elephants was associated with a substantial reduction in the abundance of bushbuck, to a third or less of their former abundance (Addy, 1993). Fire was not a factor in the river front region, being blocked by the main road paralleling the river.

Further west along the Linyanti River, a similar pattern of woodland conversion is in progress, mostly outside the national park. Extremely high local concentrations of elephants develop here during the late dry season, up to 20 elephants.km⁻². By 1991 over 40 per cent of the trees in the riparian fringe were dead (Coulson, 1992; Wackernagel, 1992). *Acacia* spp. were most severely affected, with two-thirds of *A. erioloba* and 45 per cent of *A. nigrescens* trees dead, in many cases due to debarking by elephants. Wind-throw and natural senescence were additional factors contributing to this mortality, and other species such as *Diospyros mespiliformis* and *Combretum imberbe* growing in the riparian woodland showed much less elephant damage. Repeated aerial photographs indicated a net loss rate of canopy trees of only 2 per cent per year between 1992 and 2001, but tree felling was patchy and much of this loss was concentrated in patches where *Acacia* spp. were prevalent (Bell, 1985). In compensation, an expanding shrub layer, largely of *C. mossambicense*, had developed by 2001.

While the vegetation changes brought about by elephants along the Chobe River are extremely severe, the area affected is restricted to a 20–30 km section by human settlements to the east (Kasane town) and west (Kachikau enclave). Animal populations seem to have benefited rather than being adversely affected, apart from bushbuck. Browsing pressure from impala would suppress woodland recovery even if elephants were greatly reduced in abundance. Of greater concern are the trends towards elimination of the *Acacia* component of the woodland plus severe impacts on certain other woody species developing along the Linyanti River. Biodiversity losses are not yet of major concern because of the restricted extent of these vegetation changes within the greater ecosystem context.

Amboseli National Park in Kenya

The Amboseli ecosystem covers 8 500 km² in southern Kenya, while Amboseli National Park occupies 388 km² within the central basin (Western, 2007). The present-day remnant of a formerly much larger lake generated by drainage from the slopes of Kilimanjaro holds water usually for only a few weeks after heavy rains. Soils derived from volcanic deposits are alkaline and locally saline because of the closed drainage, except around the swamp margins. Further back the vegetation grades into bushland or open woodland with *Acacia tortilis*, *A. mellifera* and *Commiphora* spp. predominating. The mean annual rainfall is 340 mm. The region currently supports a population of 1 400 elephants, with the local density within the park amounting to 2–3 animals.km⁻². Elephants formerly migrated seasonally between the basin and surrounding bushland,

and their concentration within the park increased during the late 1970s after Maasai pastoralists and their livestock were excluded from this area.

Die-offs of extensive areas of *A. xanthophloea* (fever tree) woodland that became apparent during the late 1960s were ascribed to a rising water table and consequently increased salinity in the rooting zone (Western & Van Praet, 1973), as documented also in the Ngorongoro caldera (Mills, 2006). However, enclosure plots suggest that elephant damage was the primary contributor to the demise of these woodlands (Western & Maitumo, 2004), although the contributory role of water level and salinity changes cannot be excluded. Within areas fenced off in 1981, dense stands of *A. xanthophloea* had established and reached a height of 7–10 m by 1988, while *Acacia* seedlings outside the enclosures failed to grow and declined in abundance. This indicates the potential of the *Acacia* woodland for rapid recovery in the absence of browsing pressure and other damage by elephants. The total area covered by fever tree woodlands within a 700 km² region declined from 125 km² in 1950 to 2 km² by 2002, coupled with an expansion by alkaline grasslands and scrubland of salt-tolerant *Suaeda monoica* and *Salvadora persica* (Western, 2007). Stands of palms *Phoenix reclinata* have replaced the woodland in some localities. Associated with the woodland decline has been a decrease in the abundance of browsing ungulates within the national park, although these species remain abundant outside the park. Historical records suggest that woodlands were absent from the Amboseli basin in the late 1800s and that the presence of pastoralists with their cattle had contributed to the development of the *A. xanthophloea* stands within the basin. Woodlands outside the park boundary have mostly recovered since the 1970s following the establishment of pastoralist settlements, which are largely avoided by elephants.

This case study illustrates the potential for elephants to largely eliminate a tree species forming a monospecific woodland from a region, as well as the potential of this *Acacia* species for rapid regeneration once protected from elephants. Other factors contributed to both the establishment and demise of the woodlands, and the area affected was a fairly small section of the regional ecosystem.

Subtropical thicket

Research on the impacts of elephants on the plant communities of Addo has followed a tradition of comparing elephant-occupied areas with areas where elephants have been excluded (i.e. botanical reserves). This assumed that any difference in vegetation was due to the influence of elephants. Elephants have been shown to reduce plant species richness, plant biomass, canopy height

and volume and density (Penzhorn *et al.*, 1974; Barratt & Hall-Martin, 1991; Stuart-Hill, 1992; Moolman & Cowling, 1994; Lombard *et al.*, 2001). Stuart-Hill (1992) argued that succulent thicket is adapted to the 'top-down' browsing by elephants, which maintains thicket regeneration by protecting canopy cover at ground level. In general, species abundance and richness of 75 special species (endemic-rich geophytes and low succulents – Johnson *et al.*, 1999) and two indicator species (*V. rotundifolium*, *V. crassulae* – Midgley & Joubert, 1991) declined exponentially with length of exposure to elephant browsing, halving approximately every 7 years (Lombard *et al.*, 2001). An important point is that 168 plant species identified as being entirely reliant on Addo for their conservation (Johnson *et al.*, 1999), are potentially vulnerable to elephant-driven extinction (Kerley & Landman, 2006).

The absence of effective density dependence in subtropical thicket (Gough & Kerley, 2006) is interpreted as a consequence of the aseasonal availability of high-quality forage, and it is predicted that the forage resource (and associated biodiversity) will collapse before density dependence emerges (Kerley & Landman, 2006).

Contrasts across biomes and ecosystems

The above savanna case studies span a rainfall range from arid (Amboseli, Tsavo East) to moist (Murchison Falls) savanna, and in soil fertility from fairly poor (the juxtaposition of Kalahari Sand with the Chobe riparian zone) to excessively eutrophic (the Amboseli basin). In all cases an extreme conversion of savanna structure occurred, associated with local elephant densities ranging between 2 and 4 animals.km⁻². The severe effect was limited in its extent to areas between approximately 100 km² along the Chobe River front and 4 400 km² in Tsavo East, and exacerbated in all cases by other factors compressing the elephant population within this area. The consequences for biodiversity as assessed through changes in habitat composition or species representations have not been quantified. A reduction in plant species diversity must surely have occurred locally, but not necessarily regionally. In some cases the vegetation showed its capacity to recover rapidly once the elephant pressure was reduced substantially; no irreversible threshold was passed, and the recovery time seemed to be merely 2–3 decades. Changes in animal populations appeared to be mostly relatively minor or locally restricted.

The transformation of savanna woodland into open grassland appears most typically as a feature of clayey soils where dense grass cover promotes hot fires (Bell, 1981). Examples include the Rwindi-Rutshuru plains in Kivu National

Park, Congo (Bourliere, 1965), and Maasai Mara Reserve in Kenya (Dublin *et al.*, 1990). On sandy soils allowing deeper water infiltration, many tree and shrub species have the capacity to resprout strongly from underground parts, so that the destruction of canopy trees by elephants leads to the development of a shrub coppice state (Bell, 1984, 1985; McShane, 1989). Examples of this include the Sengwa Research Area (Guy, 1989; Mapaure & Campbell, 2002) and Chizarira National Park (Thompson, 1975) and elsewhere in Zimbabwe (Holdo, 2006), as well as sections of Murchison Falls National Park and the Chobe River region, as described above. A similar conversion to a hedged or shrub coppice state has been documented for mopane woodlands, despite their prevalence on clay soils (Lewis, 1991). In South Africa the contrasts in woodland change between eastern and western regions of Kruger are consistent with this pattern (Eckhardt *et al.*, 2000). Thus, on the eastern basalts a substantial opening of the tree canopy has occurred, while on the western granites the overall woody plant cover did not change although the presence of tall trees decreased.

The studies outlined above have described general features of the consequences of elephant impacts for vegetation structure and composition, for the regions or ecosystems concerned, but some caveats should be noted. All areas show high spatial variability in these impacts as well as temporal variability. It is easy photographically to contrast local devastation with intact woodlands remaining nearby. The causes of this intense localised damage remain unknown, although Chafota's (2007) observations on interactions involving fire, frost, and the persistence of surface water shed some light on possible mechanisms. It is possible that the former pattern was a mosaic cycle of intense utilisation, with elephants moving elsewhere until areas previously heavily impacted had recovered. The extent of the area required for such a spatial pattern of utilisation to be maintained is unknown. Movement studies have merely documented opportunistic concentrations in areas where rainfall has promoted new growth, plus dry season concentrations around remaining sources of water for drinking. Tree populations within semi-arid environments seem also to recruit episodically at long intervals, during rare sequences of years with high rainfall, low fire frequency and low browsing impacts (Young & Lindsay, 1988; Walker 1989).

SPATIAL AND TEMPORAL PERSPECTIVES

The disturbing impacts on vegetation imposed by elephants are not only greater in magnitude than those due to other large herbivore species, but also extend over broader areas. The time taken by canopy tree populations to recover is

also correspondingly longer than that for grasses and other herbaceous plants. While it has been proposed that 'intermediate' disturbances are associated with the highest species diversity (Connell, 1978), defining what is intermediate is problematic. It is not only the magnitude of the effect that is important, but also its spatial extent and frequency. Severe plant mortality imposed over the whole extent of a protected area and sustained for longer than the persistence of seed or seedling banks would obviously be disastrous. On the other hand, clearing of the existing vegetation from some areas by elephants potentially opens opportunities for plant species poorly represented elsewhere to colonise, potentially enhancing overall species diversity, but only if these plants are allowed sufficient time to establish. These concepts have not been rigorously applied to the elephant-vegetation interaction.

Temporal perspectives of elephant impact are generally poorly studied. Impacts over time will have two components – that of seasonal/interannual variation in impacts, and that of the actual rate of impacts. Given the seasonal variation in grass availability, and hence diet, it is predicted that elephant impacts on woody vegetation will be higher during winter than summer. This was confirmed for Madikwe (Govender, 2005). Similarly, elephant browsing intensity on mopane is greatest after spring rains (Styles & Skinner, 2000). On an interannual scale, the Tsavo elephant impacts saga is strongly linked to drought conditions (e.g. Leuthold, 1977). In contrast, the lack of seasonal variation in diet composition (and hence presumably impacts) in Addo (Davis, 2007) reflects the evergreen nature of subtropical thicket.

Rates of change are similarly poorly studied, the best documented being for Addo. The elephant enclosure of Addo was enlarged on a number of occasions, providing areas with different periods of elephant occupancy. Using these variations in elephant density and time since exposure to elephants, Barratt & Hall-Martin (1991) showed changes in plant architecture, Lombard *et al.* (2001) showed changes in the regionally rare and endemic small succulent shrubs and geophytes, and Magobiyane (2006) estimated the rate of impact on mistletoes. These studies in subtropical thicket show that some species respond very rapidly to elephant impacts.

In the Sengwe Wildlife Research Area, Zimbabwe, annual loss of trees in the height class >5.0 m varied from 3 per cent for *Brachystegia speciformis* to 100 per cent for *Diplorynchus condylocarpon*, in the presence of elephants (Martin *et al.*, 1996), and on average tree loss rates were in the region of 22 per cent across species within Mopane and Miombo woodland (Martin *et al.*, 1996). In the Matusadona Highlands, Zimbabwe, tree loss rates of 21 per cent occurred even at low (<1 elephant.km⁻²) densities. Modelling of tree loss and

recruitment as a function of elephant density shows that very low elephant densities (0.1–0.5 elephant.km⁻²) are required to achieve equilibrium between tree loss and recruitment (Martin *et al.*, 1996).

Spatial perspectives are better understood. Elephants, like other animals, do not use the landscape in a uniform fashion and hence vary their impacts across landscapes, producing heterogeneity in biodiversity patterns. One of the major factors influencing space use by elephants is topographical relief, and Wall *et al.* (2006) showed that elephants are reluctant to climb slopes. This is expressed in reduced elephant impact in relation to topographic relief (figure 2). The consequences are that tree species that seem most susceptible to elephant impacts, such as marula and baobab, tend to be prevalent in upland regions of the landscape (Weyerhaeuser, 1985; Edkins *et al.*, 2007).

Although Tsavo East National Park is commonly advanced as an example of the devastation potentially brought about by elephants, less than a quarter of its 20 000 km² extent was severely affected. Furthermore, this was largely in the lowest rainfall region, where the effect of drought conditions was most severe (Myers, 1973). Likewise, the zone of severe impact on riparian vegetation along the Chobe River spans less than 20 km (Skarpe *et al.*, 2004).

Elephants use vegetation types differently (e.g. Guldemand & Van Aarde, 2007). Despite their reliance on grass in the diet, there is a poor understanding of their use of grasslands, with most studies comparing woodland types, largely in terms of impacts. In Madikwe (Govender, 2005) and Pilanesberg (Moolman, 2007), elephants impacted *Acacia* woodland types significantly more than *Combretum* woodland types. In Phinda, two of the top three impacted habitats were *Acacia* dominated (the other was threatened sand forest), while in Mkhuzu one of the top three impacted habitats was *Acacia* dominated (Repton, 2007). Further, some tree species were heavily used at some sites, but the same species was not heavily used at other sites (e.g. Madikwe – Page & Slotow, 2001; Pilanesberg – Moolman, 2007). In the Eastern Cape, elephants avoided karroid shrublands in Kwandwe (Roux, 2006).

The above patterns show that refugia from elephant impacts occur at a variety of spatial and possibly temporal scales, and these patterns need to be better understood. There are two further important aspects of such heterogeneous spatial patterns, firstly where elephants impact the areas around water (see Piosphere effects below), and secondly where their impacts are confined within small areas (see below).

Piosphere effects

Particularly relevant within this context is the abundance and spatial distribution of perennial surface water sources. Being water-dependent, elephants generally drink every 1–2 days (Owen-Smith, 1988), and typically forage up to about 16 km from water, although this extends up to 60 km in extreme cases (Laws, 1970; Western, 1975; Leggett *et al.*, 2003, 2004, 2006a & b). Accordingly, they concentrate near rivers or other sources of drinking water during the dry season, and disperse through a wider area during the wet season when pools are more widely distributed (Western, 1975; Thrash *et al.*, 1995; Owen-Smith, 1996; Leggett *et al.*, 2003, 2004, 2006a & b; Chamaillé-Jammes *et al.*, 2007; Smit *et al.*, 2007). The dry season concentration of elephants near surface water contributes to a gradient of intensifying impacts on vegetation, termed a piosphere, with the sacrifice zone in close proximity to the water source (Andrew, 1988). This region shows increases in soil nutrients, dung deposition, and trampling, decreases in trees and palatable perennial herbs, and increases in annual and unpalatable herbs and the amount of bare ground, soil compaction, and increased erosion (Bax & Sheldrick, 1963; Van Wyk & Fairall, 1969; Weir, 1971; Tolsma *et al.*, 1987; Thrash *et al.*, 1991, 1995; Ben-Shahar, 1993; Belsky, 1995; Owen-Smith, 1996; Thrash, 1998; James *et al.*, 1999). Piospheres may become especially intense around point sources of water such as those provided by boreholes, feeding troughs or artificial pools (Ben-Shahar, 1993; Conybeare, 1991; Owen-Smith, 1996). The availability and distribution of water sources can influence ecosystem structure and function at a range of scales and organisational levels, through its influence on various processes and feedbacks affecting both animals and plants (Gaylard *et al.* 2003; De Beer *et al.*, 2006)

Piospheres are manifested in woody vegetation primarily through changes to local structural heterogeneity by elephant browsing. Documented effects of elephants include a decrease in the density of *C. mopane* shrubs within 100–200 m of borehole sources (Fruhauf, 1997), and declines in plant species composition, density and diversity in areas close to pumped pans (Conybeare, 1991). With close spacing of water points, the regions severely affected tend to coalesce, restricting the opportunity for vegetation to recover when elephants move away, since their presence becomes effectively year-round (Owen-Smith, 1996). Waterpoints established in upland areas of the landscape may be especially detrimental, because tree species, such as marula and baobab, prevalent in these regions appear to have less capacity to recover from elephant damage (Weyerhaeuser, 1985; Edkins *et al.*, 2007). On the other hand, trees

growing along river margins have a substantial capacity to recover from floods, let alone elephant damage (Rountree *et al.*, 2000; Rogers & O'Keefe, 2003).

Episodic severe damage and patch dynamics

Much of the extreme damage by elephants to canopy trees will be imposed during restricted periods when elephants experience an acute shortage of food. In northern Botswana, three documented instances related to events associated with fire, frost and extended lack of rainfall (Chafota, 2007). In one instance elephants moved 40 km away from the Chobe River following the first spring rains, to encounter an area that had recently been burnt. In the absence of much accessible forage, over 25 per cent of trees exceeding 10 cm in basal diameter were felled within a brief period, largely by female elephants. In a second case, severe frost eliminated much of the accessible browse in the Kazuma Forest Reserve. Within a few weeks, over 50 per cent of *Brachystegia africana* and *B. boehmii* trees had been felled by a group of bull elephants frequenting this region. In the third instance, early cessation of the summer rains led to greater damage by elephants to mopane and riparian woodland trees near the Linyanti River.

These instances of severe mortality of canopy trees imposed within a limited area over a restricted period could lead to the development of a mosaic interspersion of patches at different stages of recovery. The generation of such patch dynamics through wind-throw has been recognised as contributing to the dynamics of temperate woodlands (Pickett & White, 1985), but explored little for savanna woodlands. The potential consequences of such heterogeneity in vegetation structure and composition will be considered below.

In savanna woodlands, opportunities for successful tree seedling establishment may occur at long intervals when conditions of high rainfall, low fire incidence and low browser pressure are experienced (Young & Lindsay, 1988). Dense stands of regenerating *Faidherbia albida* trees developed on islands and sandbanks in the Zambezi River in 1985 due to some unidentified circumstances, despite an abundance of elephants and other large herbivores (Dunham, 1994). The development of the riparian woodland along the Chobe River has been ascribed to the low abundance of browsing ungulates following the rinderpest epizootic towards the end of the nineteenth century coupled with the elimination of elephants by hunters (Walker, 1989). The rarity of conditions enabling tree seedling recruitment will slow the recovery of woodlands after elephants are removed or reduced in abundance.

Impacts in confined areas/small reserves

Although it may be expected that elephants will utilise confined areas in a uniform fashion, there are limited data to support this. Roux (2006) showed that for smaller reserves (<1 000 km²) range size was a function of reserve size, but not for larger systems, suggesting that smaller reserves would be used more comprehensively. Nevertheless, even within the Ithala Game Reserve (300 km²), about 50 per cent of the reserve is not used by elephants because of topography, habitat and behaviour (Wiseman *et al.*, 2004). Within the Songimvelo Reserve (310 km²), elephants use only a 120 km² section at an effective local density of 2.75 elephant.km⁻² (Steyn & Stalmans, 2001). Elephants are restricted to the eastern half of Pongola Game Reserve by a railway track bisecting the reserve (Shannon *et al.*, 2006a), and hence have an effective density of 1 elephant.km⁻². Similarly, although the entire Phinda Reserve (150 km²) is used by elephants, not all parts are used with the same intensity (Druce *et al.*, 2006). These patterns may in part be due to the relatively short periods that elephants have been confined in some small areas, as well as variations in density within reserves. In contrast, elephants have been confined to Addo for over 50 years, and despite the addition of new areas (growing from 27 to 120 km²), a clear pattern of homogeneous impacts (i.e. decline in plant richness, taking period of occupation into account) can be seen (e.g. Barratt & Hall-Martin, 1991; Lombard *et al.*, 2001; Magobiyane, 2006).

MEGAHERBIVORE RELEASE

The absence of elephants will bring about changes to ecosystems (e.g. Kerley & Landman, 2005), which is known as megaherbivore release. This complicates the interpretation of elephant impacts, as it has been argued that where elephants have been reintroduced into an area, observed changes are a return to the situation prior to elephant removal (c.f. Conybeare, 2004). Kamineth (2004) showed that in the absence of megaherbivores (including areas with historical megaherbivore records) tree *Euphorbia* populations were dominated by younger plants (<100 years), with few adults (i.e. recruiting populations). In the presence of megaherbivores (historical and current), however, *Euphorbia* populations were characterised by individuals in younger and intermediate (100–150 years) age classes (i.e. irregular age distributions). No recruiting populations were observed in the presence of megaherbivores. Thus, the presence of megaherbivores has resulted in a high incidence of adult tree *Euphorbia* mortality, and may have controlled tree numbers. This suggests

that the local abundance of tree *Euphorbias* is an artefact of relaxation from browsing or other effects provided by megaherbivores.

Skarpe *et al.* (2004) also suggest that the large populations of *Acacia* and *Faidherbia* in the Chobe area were established during periods of low herbivore biomass. The mechanisms of megaherbivore release extend beyond direct herbivory, as the absence of elephants will influence a number of ecological processes (Kerley & Landman, 2005).

CONSTRAINTS TO IDENTIFYING ELEPHANT EFFECTS

The interpretation of elephant impacts is rarely possible to do in isolation of possible confounding or synergistic effects such as fire (Trollope *et al.*, 1998; Bond & Keeley, 2005; Chafota, 2007), other herbivores (Cowling & Kerley, 2002; Skarpe *et al.*, 2004), drought (Wiseman *et al.*, 2004), wind toppling (Bell, 1985), soil chemistry and water table (Western & Van Praet, 1973; Mills, 2006), and frost (Holdo, 2007). Specifically, in Ithala, other browsers (black rhino = 13 per cent of individuals; other browsers about 30 per cent) had almost a three-fold higher effect on woody vegetation than did elephants (16 per cent). Of the top 20 plant species by canopy removed, 12 were more heavily impacted by other browsers than by elephants (Wiseman *et al.*, 2004). Note, however, that these relative impacts are not expressed in relation to browser biomass.

There are few studies that show no changes or increases in species richness or numbers of particular species (i.e. so-called 'positive effects') in response to elephants. It is, therefore, not clear as to how much our understanding of elephant impacts is biased by the possible under-reporting of such effects.

Furthermore, the studies on confined populations are complicated by the inability to control for elephant density, as opposed to elephant presence (Cowling & Kerley, 2002). Benchmarking elephant impacts is also complicated by the absence of a 'natural state' yardstick, as well as the consequences of megaherbivore release (see above). The measurement and interpretation of elephant impacts, therefore, needs to be undertaken in a rigorous fashion such that confounding effects are controlled for (Cowling & Kerley, 2002). A useful approach is to quantify impacts on a gradient of elephant density or period of occupation (Barratt & Hall-Martin, 1991). The interpretation of impacts should be based on a sound understanding of the mechanisms of such putative impacts in order to avoid the risk of incorrectly assigning impacts to elephants (Landman *et al.*, 2008).

Given the longevity of elephants, the scales at which they use landscapes, as well as the temporal and spatial scales of responses of ecosystems affected

by elephants, there are further constraints on our understanding of elephant-ecosystem interactions. Thus, the typical study (~1 year) on elephant impacts is of too short a duration (Kerley & Shrader, 2007), or too spatially restricted (e.g. Cumming *et al.*, 1997) to provide a real view of the effects. It can be predicted that elephant effects will be further confounded by the effects of climate change (Kerley & Landman, 2006), and this should be borne in mind when designing elephant-effect studies.

CONCEPTUAL/MODELLING FRAMEWORK FOR CONTEXTUALISING ELEPHANT EFFECTS

Caughley's (1976b) model describing the eruptive dynamics of a herbivore population introduced into a new environment, developing through the interaction with vegetation, has been highly influential in guiding thinking about possible long-term trajectories of elephant numbers and vegetation. The fundamental feature underlying these dynamics is the delay in the response of the vegetation to increasing levels of consumption by the herbivores. In suggesting the possible relevance of this model for elephant dynamics, Caughley (1976a) emphasised how the delayed recovery of woodlands following their depression by elephants, coupled with the delayed response of elephants to the woodland reduction (because of their capacity to use grass as an alternative food source), could lead to reciprocal cycling in abundance with a period of around 100 years. Duffey *et al.* (1999) suggested that more realistic parameter values for elephants could lead to stability rather than cycling, but incorporated a stabilising density feedback by basing the functional response on a consumer-resource ratio rather than simply resource abundance.

However, neither of these models accommodates heterogeneity in vegetation structure or composition, or temporal variability in conditions, not even the seasonal cycle of production and decay by plants, nor do they address biodiversity *per se*. Owen-Smith (2002a) demonstrated that effective functional heterogeneity in vegetation quality, coupled with adaptive resource selection by herbivores, could promote stability rather than cycling, and suggested that this finding might have some relevance for the dynamics of elephants and woodlands in terms of achieving a stable state (Owen-Smith, 2002b). However, of most relevance is the potential recovery rate of tree populations.

Baxter & Getz's (2005) model provides a foundation for contextualising the relative effects of elephants, fire and climatic variability on likely trends. This represented a 1 km² cell with woody plant growth dynamics parameters specifically based on mopane, with a relatively simple age structure of the

Box 1: Research needs

There is an urgent need to study the effect of elephants on biodiversity, specifically those aspects which are considered critical for ecosystem integrity (e.g. species level effects), or which are featured in the management objectives for specific protected areas (e.g. landscape level effects such as presence of large trees), as a function of elephant density. The observation that such impacts are often scale- and site-specific or episodic requires that this be undertaken at a range of spatial and temporal scales and at different sites varying in climate and soil features. Sampling should be designed to detect episodic effects.

The rate of change brought about by elephants as a function of elephant density is key to managing biodiversity in elephant areas, and this needs to be specifically quantified. Of value here may be the areas to which elephants have recently been reintroduced.

The mechanisms of elephant impacts need to be more clearly researched, in order to predict the consequences of increased elephant density and to ensure that management responses are appropriate. This is particularly important since interactions with other ecosystem drivers (fire, drought, other herbivores, disease) may be confounding.

It has been shown that different habitats respond differently to elephant impacts and it may be hypothesised that elephant impacts are greater in habitats where they are resource limited. Research is needed to quantify elephant resource requirements and to establish how these may be provided in different habitats in order to guide the introduction of elephants into new locations and predict risks to biodiversity and identify spatial and temporal refuges from elephant impacts.

The response of biodiversity to management interventions to reduce elephant impacts (fencing, habitat expansion, etc) is key to assessing the effects of such interventions. Research is needed to provide evidence for the success or failure of such interventions.

The effects of the absence of elephants (megaherbivore release) need to be further researched, as across South Africa elephants are no longer a functional part of most ecosystems which may be dependent on the process provided by elephants.

elephant population. They suggested that a decline in woody vegetation might occur once effective local elephant densities exceeded 1–2 elephant.km⁻². This model needs to be expanded to take into account other woody species with different growth characteristics, as well as seasonal and spatial variation in the local presence of elephants, and a better elephant population model. A model developed by Holdo (2007), specifically for miombo woodland, indicated a likely decline in woody vegetation with elephant densities of around 2 elephant.km⁻².

ASSESSMENT

1. That elephants at high densities are having an impact on plant communities, with consequent changes in vegetation structure and species composition, is undeniable. However, such changes vary in extent, rate and severity between ecosystems. There is currently no recommended density for elephants to manage such changes, and the desirability of such changes will depend on the management objectives.
2. Some plant species can cope with elephant browsing, stripping or toppling, although this varies substantially with circumstance (e.g. xeric vs. mesic savannas). Therefore, aside from a number of instances where local extirpation has occurred, the most significant impact that elephants will have is the changing of vegetation structure.
3. There are very few data on rates of change in response to elephants. This will be a function of the density of elephants, the availability of alternative resources and the nature (e.g. life history) of the component of biodiversity of interest, as well as other ecosystem drivers that are involved.
4. It is difficult to untangle the effects of elephants and confounding factors such as fire, natural plant senescence and episodic recruitment events (e.g. Skarpe *et al.*, 2004). These levels of interactions will be exacerbated by climate change.
5. Many plant populations will recover once the pressure of high elephant densities has been released; however, these rates will vary between species and landscapes and the extent of change; animal populations will respond faster, unless they are dependent on the habitat provided by the plants.

6. While extensive data are available from elsewhere in Africa, a paucity of data of elephant effects exists in South Africa. The most comprehensive data are for Addo, with limited information in northern KwaZulu-Natal and Kruger.

CONCLUDING COMMENTS

We conclude that elephants are special in the nature of their feeding, and hence their impacts, by virtue of features such as body size, the trunk and tusks. Overall, our Assessment is that while the impacts of high elephant concentrations may bring about local changes in vegetation and associated animal species, and hence local biodiversity, this need not be the case at the wider ecosystem level. Moreover, unless extreme, the consumption and breakage of woody plants and uprooting of grass tufts by elephants promotes compensatory regeneration and hence probably enhanced ecosystem productivity, as has been demonstrated for grazing systems. The concern is not the local severity of elephant impacts, which could be adverse for both productivity and diversity if extreme, but rather the persistence and extent of such pressure on plants, and the cascading or knock-on effects of elephants on other elements of biodiversity.

Transformation brought about by elephants is restricted in extent by the spatial dispersion of natural perennial surface water, where such dispersion is greater than the average daily foraging distance of elephants (c. 16 km). This is altered by the extent to which water is augmented by dams and boreholes. Elephant feeding on woody plants and grasses can facilitate feeding by other large herbivore species. Adverse consequences for these species arise through habitat transformations rather than direct competition. Prior to the large-scale changes in elephant abundance and distribution, it was recognised that elephants impacted landscapes (Selous, 1881), but unfortunately there are no benchmarks of elephant-landscape interactions in the absence of humans. This is further complicated by the recognition that elephant impacts varied in space and time. Defining the severity of impacts, and hence managing impacts, therefore will depend on management objectives for a particular system.

ENDNOTE

1. For ease of reference, we have retained the genus *Acacia*, but note that the nomenclature is under revision.

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