Elephants, woodlands and biodiversity in Southern Africa

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Elephants, woodlands and biodiversity in southern Africa

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When elephant densities exceed approximately 0.5 per km^2, savanna woodlands are generally converted to shrublands or grasslands. The impact of such elephant-mediated habitat change on biodiversity in African game reserves has seldom been measured. We examined species richness of woody plants, birds, bats, mantises and ants in reserves where elephants had destroyed the miombo woodland and in adjacent but intact miombo woodlands outside the reserves. Species richness of woodland birds and ants was significantly lower where elephants had removed the tree canopy. Our findings may have important policy implications for conserving biodiversity in many African reserves in the face of rapidly growing elephant populations (approximately 5% per annum). The problem is further compounded by international public pressures against reducing elephant densities within game reserves while, outside these protected areas, savanna woodlands and their associated faunas are being lost to agriculture. Where then will refugia for habitat-sensitive species exist if not within the region's largest protected areas?

Preserving large populations of elephants while maintaining biodiversity in national parks and protected areas in East and southern Africa is becoming increasingly problematic. In southern Africa human and elephant populations are growing at rates of about 3% and 5% per annum, respectively[1–5] and in some areas wildland is being converted to subsistence agriculture at similar rates.[6] The results are further reductions in elephant range, increased density of elephants within protected areas[7,8] and human expansion into marginal lands.[1] Together these processes are leading to the deforestation of large areas of savanna woodland of high biodiversity but low agricultural productivity.[9–11] Besides affecting biodiversity, deforestation, particularly of upland woodlands, is likely to affect seasonal patterns of water storage, discharge and stream flow from otherwise protected landscapes.[12,13]

Contrary to popular perceptions, elephant numbers were not always high in East and southern Africa and high densities such as presently occur in many national parks were seldom encountered by early explorers. In southern Africa elephant numbers reached very low levels by the 1880s due to hunting and by 1900 their extinction south of the Zambezi was considered likely.[14,15] Elephant numbers at the turn of the century in Zimbabwe, for example, were less than 5 000 and the human population was below 500 000 compared to present numbers of more than 60 000 and 11 million, respectively.[16,17]

Large generalist herbivores in the absence of their predators can have devastating effects on biodiversity; introduced domesticated species, such as goats on oceanic islands, have provided spectacular examples.[18] The African elephant is an example of a large, generalist herbivore which has often transformed natural habitats in game reserves[19–32] where it has been protected from human predation. In many East African parks and reserves widespread elephant impacts were greatly reduced during the 1970s and 1980s by illegal hunting for ivory.[33,34] In southern Africa, where elephant populations are still growing,[4,5,35] attempts by wildlife management authorities to mitigate effects on woodlands by culling elephants have been resisted by public pressure groups both within Africa and beyond.[36–41] Ecological counterarguments to culling have also been advanced[42–45] but elephant impacts on biodiversity, as opposed to their influence on vegetation structure and scenery, have seldom been considered in the debate because of the absence of appropriate studies. Recent exceptions are the studies of elephant impacts on plant species diversity of succulent thicket in the Eastern Cape of South Africa[46] and effects on bird diversity in northern Botswana.[47]

Miombo woodlands (species-rich, broad-leaved, deciduous woodlands dominated by trees of the genus *Brachystegia* and *Julbernardia*) prevail over much of southern central Africa from Tanzania south to Zimbabwe and from Angola across to Mozambique.[48] Throughout much of this region woodland has been cleared for cultivation, and in parts of the Zambezi valley in Zimbabwe this has occurred at the rate of 4% per annum over the last three decades.[6] High elephant densities, combined with fire, have had a major effect on formerly pristine miombo woodlands in many protected areas of the region and particularly in Zimbabwe, where veterinary control fences have confined expanding elephant populations to protected areas. Although elephant impact on miombo woodland structure and woody species is well known,[23–25] the effect of high elephant densities on other taxa has been neglected. We therefore compared woodland structure and biodiversity in elephant-affected miombo woodland (within protected areas) with biodiversity in equivalent, undisturbed, or intact habitats outside protected areas.

Study areas and methods

We worked in miombo woodlands in the southern escarpment of the Zambezi valley in Zimbabwe (Fig. 1). Elephants were seldom present in the intact woodlands (e.g. Fig. 1*b*) until recently, whereas elephant densities in the the affected woodlands (e.g. Fig. 1*c*) had exceeded 1 elephant per km^2 since the mid-1970s (Department of National Parks and Wild Life Management, unpub. censuses). In the Mana area (Fig. 2) intact and impacted woodlands were separated by a game fence, while in the the Kanyati/Matusadona area they were separated by the Sanyati Gorge, which is impassable to elephants. The game fence on the southern boundary of the Mana Pools National Park and the Hurungwe Safari Area was erected in 1968, as part of tsetse control operations in the region, to prevent the southward movement

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Fig. 1. Elephant impact on woodland. (*a*) Oblique aerial view of the southern boundary of Mana Pools National Park/Hurungwe Safari Area, showing elephant-affected woodland to the right (north) of the tsetse fence and intact woodland in the adjacent communal land to the south. Note clearance for agriculture in the middle distance (May 1996). (*b*) Ground view of intact miombo woodland south of the fence in Communal Land (November 1994). (*c*) Ground view of elephant and fire- affected woodland to the north of the fence inside game reserve (November 1994). (Photographs by David Cumming)

of elephant and other game into the adjacent Hurungwe Communal Lands.

In the Mana area on each of nine nights between 15 and 24 November 1994, we sampled an intact woodland site north of the fence and an impacted woodland site south of the fence to provide nine paired samples. In the Kanyati woodlands six intact sites were sampled over three nights (26–28 Nov.), followed by samples from six impacted sites, also over three nights, in the Matusadona woodlands (30 Nov.–2 Dec.). The distance between the Kanyati and Matusadona areas (approximately 40 km) precluded simultaneous sampling of intact and impacted sites.

Our sample sites were near the crests of ridges in undulating terrain and were in similar geological formations and soil types. On each sampling night two teams simultaneously sampled bats and insects at two sites and the next morning at each site we listed birds and sampled vegetation.

Woody vegetation was sampled in two ways. At each site all species, in three size classes (small shrubs <1 m; shrubs 1–3 m; trees >3 m), were recorded within an area of about 1 ha to provide a measure of species richness. The number of woody plants by species in each of the three size classes was then recorded in a 50-m-long belt-transect orientated north-south or east-west, whichever maximised overall site variability. Transect width was adjusted between 2.5 and 7.5 m to include at least 15 individuals in each size class. Overall, we identified approximately 50–100 individual plants in each transect and measured their basal diameters.[49] Basal diameters were measured to accommodate the prevalence of multi-stemmed and coppicing plants.

At each site we listed all the bird species encountered by one observer in a 45-min sampling period starting at either 05:00 or 07:00, with the starting time alternating on consecutive days between disturbed and undisturbed woodlands. Sampling time did not significantly affect the number of species of birds observed ($\chi^2 = 3.47$; d.f. = 1; $P > 0.05$). Birds, identified visually and by their songs, were recorded while walking within a radius of approximately 250 m of the previous evening's bat and insect sampling station.

We sampled flying bats using macro-mist nets[50] erected at dusk and set open from 18:30 to 23:30 when they were monitored continuously. For each captured bat, we recorded the time of capture, species and sex.

Insect samples were collected from two light traps at each sampling site: a 12-V white fluorescent neon tube suspended above a dish of soapy water and turned on from 19:00 to 20:30; and a 12-V ultraviolet neon tube suspended under a white sheet spread over a tripod of 1-m-long poles. The UV light was turned on for the first 15 min of each 30-min period (starting at 18:30). During the last five minutes insects were collected off the sheet into a wide-necked killing jar. Insects from the UV samples were sorted by size class and order. Formicids and

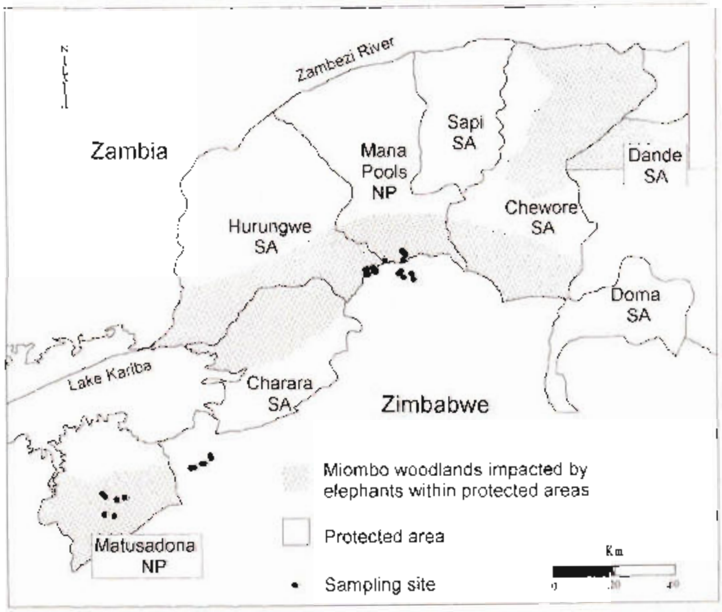

Fig. 2. Study area on the Zambezi Valley escarpment in Zimbabwe showing protected areas (NP, national park; SA, safari area) and sites sampled (l) on the southern boundary of Mana Pools National Park and Hurungwe Safari Area, the Kanyati Communal Land and the Matusadona National Park. Intact miombo woodlands within the protected areas occur in the southern part of Charara (south of former tsetse fence) and in the Doma Safari Area.

mantids from both sampling systems were separated by species. We lacked the resources to separate other insect taxa to species level.

Results

Woodland structure differed markedly between impacted and intact woodlands (Table 1). Tree cover and the density of large trees (basal diameter >15 cm) was markedly lower in affected sites. Differences in mean overall tree density were not as high because some sites, particularly in the Matusadona, had high densities of small, regenerating, *Brachystegia boehmii* trees. Associated with reduced tree cover in impacted woodlands was a nearly fourfold increase in shrub cover and a twofold increase in small-shrub cover (Table 1). Neither the mean number nor the overall number of woody plant species found in intact and impacted woodland differed significantly but the number of woody species in the >3-m height class, namely trees, was markedly lower in the affected woodland (Table 1).

Significantly fewer bird species were found in impacted woodlands and, as expected, the greatest contrast in species richness was found in woodland species where species richness was significantly lower in impacted woodland (Table 1). We recorded a total of 121 species of birds with a total of 99 species in intact woodland and 73 in impacted woodland. The loss of woodland species in affected areas was not compensated for by an increase in non-woodland species (Table 1). Among the arboreal passerine bird species present in the intact woodland but missing from the impacted woodlands were four miombo woodland endemics (Miombo Rock Thrush, *Monticola angolensis*; Spotted Creeper, *Salpornis spilonotus*; Mashona Hyliota, *Hyliota australis*; Miombo double collared Sunbird, *Nectarinia manoensis*; Cabanis's Bunting, *Emberiza cabanisi*) and several species which, although occurring in other habitats, might be described as miombo woodland specialists in the sense that their distribution is largely confined to this habitat type.[51,52]

We captured a total of 344 bats and, because all of the adult females were lactating or post-lactating, the populations appear to be resident and breeding. Bat species richness in upland areas was low with 11 species being caught over 15 nights of trapping, while the greatest number of species caught at any one site was eight. The number of bat species caught in intact and impacted woodlands did not differ significantly (Table 1). Fruit bats (*Epomophorus* species) were caught only in intact woodland while seven species of vespertilionids were caught in both intact and impacted sites.

We consistently caught more species of ants by night in the intact woodland in the Mana area and the same pattern prevailed for mantises; these patterns were less marked in the Kanyati and Matusadona sites (Table 1). We found and heard cicadas only in the intact woodlands and seven specimens from two genera (*Lacetes* and *Oxypleura*) were captured at the light traps.

Discussion

Our results show that where elephants have existed at high densities (>0.5 per km^2) for more than a decade (Cumming and Taylor, unpublished census data) the structure of woodlands is changed markedly and the diversity of canopy trees and of associated bird and insect faunas may be reduced. Most woody species were still present in the shrub layer and the potential for regeneration of the woodland, albeit via a thicket phase, was still present. Bird species diversity is known to be correlated with foliage height diversity in woodlands[53,54] so that the greatly reduced vertical and horizontal heterogeneity in the elephant-affected woodlands would account for the lower species richness of birds in these woodlands.

While frequent hot late dry-season burns can open up miombo woodlands[55] in the absence of elephants, it is the interaction of elephants and fire that is of prime importance in the context of our study areas. Since the onset of tsetse control operations in the mid-1960s, intact miombo woodlands in the Mana and Kanyati areas were subjected to early burns and elephants were removed. Within the national parks (impacted areas) confined elephant populations increased and unsustainable rates of tree felling were evident by the late 1960s and early 1970s (personal observation and blanket aerial photography). Attempts in the early 1970s to protect woodlands from fire only served to increase the risk and frequency of late hot burns[56] because wild fires could seldom be controlled. An early-burning policy was introduced to pre-empt the risk of hot, late season burns but was not consistently implemented in the Mana area. In the Matusadona highlands early burning combined with a reduction in elephant numbers facilitated the regeneration of *Brachystegia boehmii* in some areas (R.D. Taylor, unpublished data). A similar reduction in elephant numbers but without an effective early burning regime in the Mana Pools National Park inhibited regeneration. The persistence of large tracts of intact woodlands south of the Mana fence, where fire was not controlled but from which elephants were excluded, is consistent with the conclusion that high elephant densities were primarily responsible for transforming closed canopy miombo woodlands to open bushlands or grasslands.

Local loss of biodiversity under high elephant densities has important implications for the role of such game reserves in conserving biodiversity locally, nationally and regionally. Elephant numbers in southern Africa presently exceed 170 000 with more than eight populations of over 5 000 animals living in reserves of more than 5 000 km^2.[57] With a probability of >99% that an elephant population of 2 500 held at 50% of carrying capacity (i.e. at a density of 0.5 elephant per km^2 in a 5 000 km^2 reserve) will

Table 1. Comparison of woody plant density and cover and species richness of woody plants, birds, bats, ants and mantises in intact and elephant-impacted woodland sites. (*A*) Tree and shrub density (density of woody plants in three height classes and large trees where basal diameter (BD) > 15 cm); (*B*) woody plant cover reflected by basal area; (*C*) species richness of woody vegetation, birds, bats, ants and mantises. (Means ± standard error of mean, n = 15 intact and 15 impacted sites (see text) except for birds where n = 14; probabilities for single-sided, 2-sample t-test; ns indicates not significant at 5% level.)

Group or taxon	Intact woodland (mean ±s.e.m.)	Impacted woodland (mean ±s.e.m.)	Probability	Direction
A) Density woody plants (plants ha^{-1})				
Trees (>3 m)	408 ± 39.9	245 ± 70.9	<0.05*	⇓
Trees with BD > 15 cm	193.8 ± 19.9	56 ± 22.0	<0.001***	⇓
Shrubs (1–3 m)	257.8 ± 44.9	1412.0 ± 209.5	<0.001***	⇑
Small shrubs (<l m)	3482.7 ± 391.9	6029.3 ± 724.4	<0.01**	⇑
B) Woody plant cover (basal area m^2 ha^{-1})				
Trees (height >3 m)	9.5 ± 1.2	3.5 ± 1.2	<0.001***	⇓
Shrubs (height 1–3 m)	2.5 ± 0.7	12.4 ± 1.8	<0.001***	⇑
Small shrubs (height <l m)	7.1 ± 0.9	15.4 ±2.0	<0.001***	⇑
C) Species richness (no. species per site)				
Trees	25.5 ± 1.0	11.2 ± 0.8	<0.001***	⇓
Shrubs	35.6 ± 1.8	35.5 ± 2.8	>0.5 ns	⇔
Total woody plants	41.1 ± 2.3	29.5 ± 3.8	>0.2 ns	⇓
Woodland birds	16.3 ± 2.0	10.2 ± 0.5	<0.001***	⇓
Other birds	5.7 ± 0.5	8.7 ± 1.1	>0.2 ns	⇑
Total birds	22.0 ± 2.3	18.8 ± 1.3	<0.01**	⇓
Bats	3.5 ± 0.6	3.3 ± 0.8	>0.05 ns	⇓
Ants	9.2 ± 0.7	7.3 ± 0.5	<0.05*	⇓
Mantises	3.0 ± 0.3	1.8 ± 0.5	>0.09 ns	⇓
Total animals (birds, bats, ants & mantises)	37.7 ± 3.2	31.3 ± 2.0	<0.01**	⇓

be genetically and demographically secure for 1000 years,[58] there is no compelling *conservation* argument to increase elephant numbers and densities in reserves within the region. Lower elephant densities (i.e. at ≤0.5 elephant per km^2) may, on the other hand, conserve higher levels of plant and animal biodiversity, safeguard habitats and reduce the risk of local population collapses of elephants or other species, or both. Examples include the initial collapse of elephant and black rhino populations in Tsavo National Park[59–61] and the extinction of bushbuck and lesser kudu from Amboseli National Park as a result of elephant-induced habitat change.[62]

The intermediate disturbance hypothesis[63,64] provides an appropriate theoretical framework within which to explore the effects of elephant disturbance on biodiversity and particularly their effects on spatial and temporal heterogeneity of habitats but this work has scarcely started.[65–67] The links between overall elephant population density (as used here), temporal and spatial shifts in local population densities and heterogeneity in woodland habitats need further examination. It is already clear that localised woodland damage and loss of certain tree species will occur even at elephant densities of <0.2 elephant per km^2 in a wide range of woodlands.[5,35] At persistent densities >0.5–1 elephant per km^2 large areas of several types of woodland have been reduced to scrub with an associated loss in spatial heterogeneity.[19–29] In Zimbabwe, localised culling in such circumstances reduced elephant densities and resulted in regeneration and a return of some spatial heterogeneity (Cumming and Taylor, pers. obs.). At the other end of the spectrum 'old growth' woodlands may well support a characteristic fauna and flora which needs to be conserved but this question has not surfaced in the elephant/woodland debate.

An alternative thesis holds that eruptions of elephant populations, woodland clearance and elephant die-offs are 'natural' and necessary for protected areas to maintain habitat resilience, stability and biodiversity in the long term (e.g. ref. 42). This view assumes, *inter alia*, that such cycles occurred naturally in the past, were sufficiently localised to avoid regional mass extinctions, and that refugia existed (and will exist in the future) from which species can re-invade habitats destroyed by elephants. However, none of these assumptions holds for our study area. The Zambezi Valley, Great Zimbabwe in the Save River catchment, and Mapungubwe south of the Limpopo were an integral part of the ancient trade in gold and ivory which was centred on the East African coast.[68–70] Ivory was harvested and traded in southeast Africa at surprisingly consistent levels over at least four centuries before the over-exploitation of African elephants occurred in the late 19th century.[71] The writings of early hunters and explorers provide no evidence that densities of 1–3 elephant per km^2 were prevalent in East and southern Africa and we are not aware of any evidence to support the view that elephants existed at high densities over extensive areas in prehistoric times. It is thus very likely that intact miombo woodlands persisted over large areas for at least the last 500–1000 years, and, given current levels of endemicity, did so for very much longer.

Presently about 88% (6 800 km^2) of the miombo woodland in protected areas of the Zambezi Valley in Zimbabwe has been heavily impacted by elephant with spatial heterogeneity largely obliterated. Only the Doma Safari Area (945 km^2) remains relatively intact (Cumming and Taylor, pers. obs.). With woodlands outside protected areas being converted to agriculture at about 4% per annum,[6] the opportunity for species re-invasions to occur from intact refugia within Zimbabwe will soon be lost. A woodland regeneration time of several decades further reduces the chances of re-invasion.

The practical problems of reducing elephant densities in large populations such as now occur in many game reserves, and other woodland habitats, in southern Africa are daunting. To reduce densities to <0.5 elephant per km^2 within Zimbabwe's protected areas, it would now be necessary to remove more than 35 000 elephants. One costly option is to move herds into new reserves or open new areas into which elephants can disperse. Both have been used in southern Africa but the scope for further translocations within the region is limited and the gains short-lived because confined, protected elephant populations soon reach levels at which they start to impact on woodlands. Culling, an option successfully used in the past, is now inhibiting because the CITES ban on trade in elephant products precludes the sale of ivory and hides and thus the opportunity to recover the costs of culling elephants. Animal welfare groups have campaigned against the use of culling, arguing instead for the use of contraceptives. For elephants this alternative has yet to be developed and tested.

Our results and this overview of the elephant problem highlight the potential risks to biodiversity conservation in African savanna game reserves of maintaining high elephant densities. The generality of our specific findings for miombo needs to be critically examined for other savanna woodland types in the region and further research on this question is urgently needed if the current impasse between protecting elephants and conserving woodland biodiversity is to be resolved rationally. Equally important is the observation that while miombo woodlands and their associated biodiversity are at risk within game reserves, woodlands outside of protected areas are also under siege from agricultural development despite the obvious long-term, adverse consequences for people and biodiversity of subsidising agricultural development on marginal soils.

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