We review available information on the impact of elephants on the Subtropical Thickets of the Eastern Capeprovince as a contribution to the current debate around biodiversity and the need to manage elephant populations. This ecologically diverse region historically supported an abundance of elephants that was incrementally reduced to a single population limited to the Addo Elephant National Park (AENP). The results of research on elephant impacts associated with this population has shown that these animals influence many ecological processes, and patterns, including soil features, landscape patchiness and plant biomass and diversity. Furthermore, elephants influence insect, bird and antelope abundances and reduce browse availability for black rhinoceros. We conclude that elephants affect biodiversity at all levels investigated but that further research is necessary to identify the mechanisms responsible. Of specific concern is the observation that the AENP represents the only current example where elephants may be driving many endemic plants to extinction. This suggests that managing elephant impacts in Subtropical Thickets, specifically, is a matter of urgency.

Introduction

The management of elephants, Loxodonta africana, in conservation areas has faced policy- and decision-makers with burgeoning populations and the loss of biodiversity,23 giving rise to the so-called ‘elephant problem’.1 Elephant management is particularly challenging given the high costs and strong public emotions elicited by culling, contraception and translocation (see Whyte et al.3). Furthermore, the information on which managers base decisions is frequently contradictory, and overviews of elephant impacts on savanna landscapes have only recently become available.22 Understanding the effects of elephants in South Africa has focused on these savannas, despite the fact that these animals are habitat generalists and historically have occurred in all South Africa’s biomes except deserts.9 Elephant moves between these biomes are characterized by the ready availability of elephants.

Elephant play a key role in ecological processes in the Subtropical Thickets of the Eastern Cape.5-21 We review the studies on elephant impacts in these thickets, in order to contribute to the larger debate. If we are to manage and conserve Eastern Cape thicket successfully, we need to develop appropriate elephant management strategies based on a sound scientific understanding which is influenced by and reflects the history of elephant exploitation, conservation, research and management in the Eastern Cape. We include background information to contextualize this synthesis.

History of elephants in the Eastern Cape

Historically, elephants occurred at high densities in the Eastern Cape, particularly in the thicket vegetation east of the Gamtoos River.4,12 Soon after Europeans settled in the Cape, these elephant herds attracted hunter/explorers in search of ivory. This resulted in a rapid eradication of the animals from over 90% of the land before any real details of their ecology were documented.

The Eastern Cape is the interface between summer and winter rainfall systems. Together with geologically and topographically complex landscapes, this results in a complex interdigitation of all seven of South Africa’s biomes in the province, which complicates our understanding of elephant ecology in the region. Boshoff et al.13 postulated that elephants occurred at high densities on the coastal lowlands and along the river valleys, where there was abundant forage and water. The interflues would have been used relatively ephemerally, given the low frequency of surface water. Boshoff et al.12 also hypothesized that elephant movements between valley systems took place on the coastal lowlands or along the more densely vegetated escarpment. A recent reconstruction of elephant distribution and densities within the area of the Subtropical Thicket Ecosystem Planning (STEP) project suggests that elephant abundance varied considerably between the different vegetation types.13 This would undoubtedly have influenced the relative impact of elephants across these landscapes, but information on this is not available.

By the end of the 19th century, the once vast population of elephants in the Eastern Cape was reduced to a single herd in the Addo bush. This herd, then estimated at about 140 individuals, was the largest of the four remaining herds [others being at Knysna, the Kruger National Park (KNP) and Thembel in South Africa.19 Through an active attempt at eradication, the population was further reduced to about 16 animals in 1919.18 Ongoing attrition through contact with humans reduced the population to 12 animals in 1931, at which time the Addo Elephant National Park (AENP) was established.18 Mortalities of the unfenced population remained high, so that when the AENP was finally fenced (an area of 23.3 km2) in 1954, the population was just 22 animals.14 Subsequently, the population has grown significantly (Fig. 1), and now numbers over 440 individuals. In response to the expanding population, the area available to elephants has been increased17 on six occasions and now exceeds 250 km2. These expansions form part of a programme aimed at establishing a mega-reserve of over 3000 km2, which includes five of South Africa’s seven biomes.18 Although historically focused on the conservation of elephants, current policy for the AENP treats the elephants together with other forms of biodiversity and recognizes the need to maintain elephant populations as an integral part of the patterns and processes required to minimize the loss of biodiversity.19

In the last decade, elephants have been re-introduced into 11 private nature reserves — Amakhala, Asante Sana, Blaauwbosch, Hopewell, Kariega, Kuzuko, Kwandwe, Kwantu, Lalibela, Pumba and Shamwari — in the Eastern Cape in response to the burgeoning ecotourism industry.2 The process has been facilitated by the ready availability of elephants.

Subtropical Thickets of the Eastern Cape

Subtropical Thicket has recently been recognized as a biome in its own right.21 These thickets are characteristic of the hot, semiarid river valleys of the Eastern Cape, where annual rainfall varies from 200 mm for arid thicket types to 1050 mm for coastal
forest thicket mosaics, and are typically dense, low-growing (3–5 m), spinescent, evergreen and dominated by woody shrubs. The importance of succulent plants varies among the 112 thicket types in response to variations in altitude and rainfall. Thickets are characterized by a high degree of endemism, particularly among the geophytes and low-growing succulents.

Historically, Subtropical Thicket supported a high diversity of vertebrate browsers, ranging in body size from the blue duiker (Philantomba monticola) to elephant. The nutritious, evergreen and spinescent nature of the vegetation has led to hypotheses of co-evolution between the vegetation and associated browsers. These landscapes are, however, vulnerable to desertification in response to inappropriate herbivore management.

**Elephant research in the Eastern Cape**

Other than for research conducted in the AENP and records of re-introduction, there are no published studies on elephants in the Eastern Cape. Consequently, our understanding of the role of elephants in the province is limited to a single population in a few vegetation types. Given the 112 vegetation types described for Subtropical Thicket, considerable caution should be used when extrapolating these findings.

Elephant research in the AENP has focused on either the elephants or their impacts. Elephant-focused work has described population demographics, ranging in body size from the blue duiker (Philantomba monticola) to elephant. This research is crucial to understanding the background to the elephant impacts, but is frequently not couched in terms of these effects. It is significant that the AENP elephant population has been growing at an average annual rate of 5.8% (Fig. 1), close to the theoretical maximum.

Research on elephant impacts in the AENP was pioneered by Penzhorn et al. and has followed a tradition of comparing elephant-occupied areas (the elephant enclosure) with a suite of sites within the AENP protected from elephant browsing (so-called ‘botanical reserves’—reviewed below). This approach assumes that the botanical reserves represent a ‘control treatment’, which can be used as a baseline to assess the impacts of elephants on thicket vegetation. This assumption may not be realistic, however, since areas protected from megaherbivore [elephant and black rhinoceros (Diceros bicornis)] browsing may experience ‘megaherbivore release’, whereby plant and animal communities may develop differently in the absence of megaherbivores (cf. Stuart-Hill, Kerley et al.).

Since the AENP population was fenced in 1954, elephant densities, ranging between 1.0 and 4.1 km\(^{-2}\) (Fig. 1), have consistently been above the recommended carrying capacity. Two estimates of carrying capacity appear in the scientific literature. Based on a comparison of elephant densities in areas of Africa with similar rainfall, Penzhorn et al. recommended that densities in the AENP should not exceed 0.4 km\(^{-2}\). More recently, Boshoff et al. using a forage production approach with modelled potential herbivore communities, estimated an ecological carrying capacity of between 0.25 and 0.52 km\(^{-2}\) for the AENP. Thus, even the lowest density of elephants since fencing of the AENP has been more than double than published estimates of carrying capacity (Fig. 1). These estimates are attempts to identify herbi-

**Role of elephants in Subtropical Thicket**

Despite their bulk and status as a keystone species, elephants do not influence all aspects of ecosystem functioning: for example, they do not act as predators. An understanding of their effects depends on appreciating their roles in the ecosystem and the associated mechanisms involved. Boshoff et al. showed that elephants played a role in 14 of 19 broad ecological processes important in thicket (Table 1). This contrasts with a smaller species such as blue duiker, which contributed to only five such processes.

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 — 146 plant species in the AENP. This is nearly five times the species consumed by coexisting ruminant browsers, like
kudu, bushbuck, or eland (*Taurotragus oryx*), and is approached, at 120 species, only by the black rhinoceros. Elephant foraging will, therefore, influence the fate of more plant species in the Eastern Cape thickets than any other mammal herbivore.

**Impacts of elephants in the AENP**

If we are to understand the impacts of elephants, the connections between the animals and their consequences need to be clearly understood and demonstrated. For example, for over 30 years the observation that *Aloe* species were disappearing in the elephant enclosure was assumed to be a response to elephant herbivory even though aloes are generally recognized to be unpalatable. Only in 2004 did Davis show that elephants actually consume aloes in limited quantities in some seasons. Elephant impacts are observed at a range of levels, from soils to coexisting mammals (reviewed below), and in all instances of such effects, the mechanisms need to be clearly identified.

**Soil resources**

Using Landscape Functional Analysis, Kerley et al. measured micro-topography and soil nutrients in the AENP elephant enclosure and botanical reserves. They showed that in the elephant enclosure there was a decline in the proportion of the landscape that represented run-on zones, where resources such as water, litter, soil and nutrients are trapped during overland flow, while the proportion of run-off zones where these resources are lost, increased. The consequences were a decline in soil nutrients. Given the lack of replication in this study, it is not possible to demonstrate that these effects were significant or due to the elephants. Kerley *et al.* however, suggested that the effects of elephants were less deleterious than those of goats. These studies must be repeated in order to assess whether elephant impacts do in fact cause dysfunctional landscapes, and at what elephant densities this occurs.

**Litter production**

One of the consequences of their feeding style is that elephants tend to discard large amounts of plant material without ingesting it. Paley estimated the amount of this material within the AENP (27 000 kg/day) as comprising two-thirds of the then estimated daily food requirements of the elephants. This, in turn, represents approximately 20% of the estimated total litter production (excluding faecal material) in Succulent Thicket in the absence of elephants. The elephant-discarded material is typically much coarser than the normal litter, and differs in terms of nutrients. Thus, elephants appear to significantly alter the size, nutrient levels and dynamics of litter in thicket vegetation.

**Landscape patchiness**

Kerley *et al.* postulated that thicket vegetation is adapted to small-scale disturbance patches, such as those brought about by elephant feeding and trampling. Elephants have been observed to create open patches where they excavate soils to practise geophagy in Addo, or where they trample the vegetation around small ephemeral water bodies (G.H.I.K., pers. obs.), but this has not been quantified.

Using population data and period of elephant occupation associated with the expansion of the elephant enclosure, Landman assessed the accumulated elephant presence (expressed as ‘mean elephant density/yr’) on the development of open habitat patches as opposed to dense thicket. She showed a significant increase in the proportion of the landscape transformed into path or open habitat with increasing elephant presence. The number of paths initially grows with increasing elephant occupation, but ultimately declines as the paths coalesce to form larger open patches. These changes had significant consequences for browse availability (see later), but have not been further investigated. It may be postulated that path formation has important knock-on-effects by virtue of changes
in microclimate associated with the change in vegetation density. In accordance with this suggestion, Henley showed that the air and soil temperature ranges of such open habitat are more extreme than that of intact thicket. The change in microclimate has unknown implications for ecosystem processes ranging from soil litter processes (cf. Lechmere-Oertel) to plant and animal physiology, seedling germination and survival.

**Impacts on plants**

The impact of elephants on the vegetation of the AENP was first recognized by Penzhorn et al. They assessed the richness and biomass of plants inside and outside the elephant enclosure and assumed that any difference in vegetation was due to elephants. Penzhorn et al. showed that total plant biomass was significantly reduced (by 55%) within the enclosure. The mean mass of Portulacaria afra, Schotia africana, Arthria tetracantha and Eucaulunda undulata was less than half of the mass outside, while that of Capparis sepiaria increased by 50% in the enclosure. Although species richness did not differ significantly between treatments, at least two species, a tree aloe, *Aloe africana*, and the epiphyte, *Viscum rotundifolium*, were absent from the enclosure.

Following the findings of Penzhorn et al., the elephant enclosure was enlarged on three occasions from 1977 to 1984, to reduce elephant density and thus their influence on the vegetation. Using these variations in elephant density and the time elapsed since exposure to the animals, Barratt and Hall-Martin compared the canopy height and crown diameter of plants and elephant damage, expressed as a function of canopy volume, in the elephant enclosure and botanical reserves. There was a significant reduction in canopy height and volume inside the elephant enclosure during 1977, while in the botanical reserve the canopy volume increased. Canopy height and volume decreased in newly incorporated areas, tending towards the 1977 estimates of the original elephant enclosure. Barratt and Hall-Martin hypothesized that areas exposed to 20 years of elephant utilization appeared to reach a loose equilibrium between plant biomass loss due to elephant browsing and total biomass regeneration. Cowling and Kerley, however, pointed out that it would be difficult to test this statement as elephant density and, therefore, browsing intensity, fluctuated in these areas over this period. The percentage of plants newly damaged by elephants was species dependent, with *P. afra* experiencing significantly more damage than *S. africana*, *E. undulata*, *A. tetracantha* and *C. sepiaria*. Barratt and Hall-Martin confirmed the disappearance of *A. africana* from the elephant enclosure as well as a significant decrease in species richness.

The disappearance of *V. rotundifolium* from the elephant enclosure, observed by Penzhorn et al., prompted an investigation into the size and frequency of the common mistletoes (*Moquinella rubra, V. rotundifolium, V. crassulaceae, V. obscurum*) and their associated host plants inside and outside the enclosure. Midgley and Joubert observed that despite the high incidence of host plants in the enclosure, all mistletoes were nearly locally extinct, while the frequency of mistletoes outside the enclosure ranged from 7% (*V. rotundifolium on Acacia karroo*) to 77% (*V. rotundifolium on *Magncus heterophylla*). Given their high nutritional status, mistletoes are thought to be selected by browsing herbivores and may therefore be useful indicators of browsing intensity.

Stuart-Hill expanded the debate on the impact of elephants, contrasting the effect of elephants and goats on the shrub component of Succulent Thicket. Using a snapshot natural experiment, he identified three browsing treatments in and around the AENP (predominantly elephant or goat browsing and browsing exclusion in botanical reserves), and compared the frequency, percentage canopy cover and density of 23 shrub species within each treatment. Results suggested that elephants and goats had a noticeable effect on the density and cover of trees and shrubs, with goat browsing being considerably more detrimental. Relative to botanical reserves, elephant browsing significantly increased (with the exception of *P. afra*) the density of the woody component, while significantly decreasing woody canopy cover. Although elephant browsing did not reduce woody species richness, it limited the variation in floristic composition to only a few species (*P. afra, C. sepiaria, E. undulata, S. africana*) and caused a significant decrease in the frequency of *Euphorbia mauritiana* (82%). *Rhigozum obovatum* and *Crassula ovata* showed a relative decrease of greater than 50% in response to elephant browsing, but this was non-significant. In contrast to these findings, Stuart-Hill argued that Succulent Thicket is adapted to the ‘top-down’ browsing by elephants, thereby maintaining thicket regeneration by protecting cover at ground level, and facilitating coppicing and vegetative reproduction, particularly for *P. afra*.

An important component of Succulent Thicket in conservation terms is the endemic-rich geophyte and low succulent flora, particularly *Crassulaceae* and Mesembryanthemaceae. Moolman and Cowling contrasted the impact of elephant and goat browsing relative to control sites on the cover and richness of this endemic component in three micro-sites: open, under *P. afra* shrubs, and under *E. undulata* shrubs. Because thicket is thought to be adapted to the ‘top-down’ browsing by elephants, but not the ‘bottom-up’ browsing by goats, Moolman and Cowling postulated that elephants will have less impact on the endemic-rich flora than goats. Furthermore, the mosaic of open and dense thicket associated with elephant-browsed thicket was thought to result in a more diverse endemic-rich flora than would be found in either control or goat-browsed sites. Due to their large bite sizes, elephants were expected to be less likely to select low succulents and geophytes. The results, however, indicated that only 12 of the 19 endemics identified occurred in elephant-browsed sites. Generally, species richness, density and cover were lower in elephant-browsed than in control sites. The cover of the *Crassulaceae* was, however, higher in the elephant-browsed treatments, possibly due to their palatability and ability to reproduce vegetatively with a consequent resilience to elephant browsing. Based on the above findings, Moolman and Cowling suggested that elephant densities should be reduced to alleviate the impact they have on the geophyte and low succulent shrubs of Succulent Thicket.

In addition to those already proclaimed, Lombard et al. identified a system of potential botanical reserves in the AENP that would conserve the components of the flora with high conservation value mostly low-succulents and geophytes, which are apparently particularly vulnerable to elephant browsing. They showed that the length of exposure to elephant browsing had a strong impact on the richness and abundance of 75 special species (Albany Centre Endemics, Red Data Book taxa, taxa very rare within the AENP) and two indicator species (*V. rotundifolium, V. crassulae*) of elephant browsing intensity. In general, species abundance decreased with increasing length of exposure to elephant browsing, with most special species recorded at low densities after 20 years of browsing, and more than half of the these species confined to small populations after 42 years of browsing. Thus, they showed that species richness for Spekboomveld declined exponentially with length of exposure to elephant browsing, halving approximately every 7 years.
Similarly, Bontveld exposed to 13 years of browsing showed a 7-fold decrease in species richness when compared with un-browsed Bontveld. Lombard et al.\textsuperscript{1} concluded that at current densities, elephants had an adverse effect on plant species diversity, with the endemic and threatened component (special species) of Succulent Thicket being most vulnerable to elephant impacts. An important point is that 168 plant species identified as being entirely reliant on the AENP for their conservation\textsuperscript{32} are potentially vulnerable to elephant-driven extinction. It is generally assumed that elephant herbivory is the primary mechanism responsible for plant extirpation in the AENP. The diet of elephants in Succulent Thicket has largely been inferred from plant-based studies,\textsuperscript{17,33} assuming that differences between botanical reserves and the elephant enclosure are due to elephant browsing. However, plants previously thought to disappear due to herbivory,\textsuperscript{34,40} do not occur in the diet of elephants despite being available. Hence, it may not be valid to attribute the disappearance of these plant species from the elephant enclosure to elephant herbivory, and alternative mechanisms of impact should be identified (see later).

Seed dispersal

Despite their dietary breadth, elephants are relatively poor seed dispersers, spreading only 21 plant species through endozoochory.\textsuperscript{7,14} In this regard they are nearly matched by black rhinoceros (20 species) and eland (20 species\textsuperscript{27}). The mechanism for this relatively poor seed dispersal in terms of species richness is not clear but may reflect the rarity of most plant species in the diet (only 25 out of 146 species comprise 71\% of the diet\textsuperscript{18}), selective foraging behaviour in terms of plant growth and reproduction patterns, the complete loss of propagules during digestion or inadequate sampling. The large volume of forage intake, and hence faecal output, by elephants,\textsuperscript{41} however, allows them to disperse large numbers of seeds.\textsuperscript{35} It may therefore be predicted that elephants play an important role in the regeneration of those plant species for which they do disperse seeds (cf. La Cuck\textsuperscript{16} for the role of black rhinoceros), but this remains to be quantified.

Insects

Musgrave and Compton\textsuperscript{46} measured phytophagous insect feeding damage on five plant species inside the AENP elephant enclosure and compared this to data for the botanical reserves. They demonstrated a significant increase in feeding damage in the presence of elephants and attributed this to an increase in the quality of browsed plants through a decline in secondary chemical compounds, for example, tannins. This hypothesis is yet to be tested. Nor was it shown which insect species were involved in this feeding process and what their population or overall insect biodiversity responses were to the presence of elephants. The postulated increase in nutritional quality of plants needs to be weighed against the significant decline in overall plant phytomass (mentioned above).

Vertebrates

Besides the work by Landman on black rhinoceros foraging opportunities (see below), the effects of elephants on other herbivores have not been directly investigated. Kerley et al.\textsuperscript{25} hypothesized that elephants may increase habitat availability for tortoises through their creation of open habitat patches and paths. This was based on Mason’s\textsuperscript{54} demonstration that leopard (Geochelone pardalis) and angulate tortoises (Chersina angulata) both preferred thicket margins and open habitats and avoided dense thicket. While it is clear that tortoise densities are relatively high in the AENP, this hypothesis has yet to be tested. Kerley et al.\textsuperscript{37} further suggested that some of the changes in the plant community attributed to elephants (declines in geophytes and small succulent shrubs), may in fact be due to an increase in tortoise access. This followed from observations that many of the plant species identified as being at risk of extinction in the AENP are preferred dietary items for tortoises.\textsuperscript{38} If this is correct, the ‘elephant problem’ may in part translate into a ‘tortoise problem’!

Chabie\textsuperscript{39} showed that in transformed thicket in the AENP, 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 species in transformed thicket. The hypothesis that elephants drive these changes needs to be further tested. Sigwela\textsuperscript{40} compared the diet of kudu in the elephant enclosure and botanical reserves and showed that elephants had no apparent effect on kudu diet selection. This is surprising given that extensive vegetation changes have occurred in the elephant enclosure, that kudu diet (28 species) includes many of the plant species recorded as being affected by elephants, and elephants consume all the plant species recorded in the diet of kudu. This suggests that dietary items are not limiting to either kudu or elephant at the present densities of vegetation and browsers at these sites.

Cape grysboek (Raphicerus melanotis), busbuck and bushpig (Potamochoerus porcus) numbers in the AENP elephant enclosure have declined over the last decade;\textsuperscript{60,61} this is postulated to result from observed changes in habitat structure brought about by elephants.\textsuperscript{62} It is not, however, known whether populations of these species outside the elephant enclosure remained constant over this period, or whether the changes in habitat structure are definitely the result of elephant impacts or whether some other process, such as global climate change, is responsible. Despite these caveats, Novellie et al.\textsuperscript{63} claimed that ‘elephants could reduce the diversity of mammal species.’

Elephants may impact biodiversity directly by killing individuals of other animal species. The killing of white and black rhinoceros in savannas by elephants has been documented and attributed to aberrant behaviour brought about by unusual population structures.\textsuperscript{62,63} Elephants are known to kill black rhinoceros in the AENP (two black rhinos were so killed in 1997 and 1998), which depressed rhinoceros population growth rates.\textsuperscript{64} There is no other evidence for aberrant elephant behaviour in the AENP, so this killing may represent an extreme form of interference competition, in which access to limiting resources is curtailed through behavioural interactions between competitors. The causes and significance of this interaction need to be further examined.

The reduction of vegetation cover and density by elephants results in a change in potential browse availability for black rhinoceros. The increase in elephant paths associated with expanded 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 (M.L., unpubl. data). Given that kudu display similar feeding behaviour to that of black rhinoceros,\textsuperscript{26} a similar response may be predicted for them. The over-utilization of thicket vegetation by elephant, therefore, compromises the potential of this vegetation type to contribute towards black rhinoceros foraging, and hence conservation opportunities. Conflict prevails between the management and conservation of these two megaherbivore species, which needs to be recognized and managed.
Ecological cascades

Given the abundance and generalist feeding behaviour of elephants and the resultant diversity of impacts in the AENP, it can be expected that elephants have a number of cascading effects on their ecosystems. One example of such an effect could be the improved access for tortoises to otherwise impenetrable thicket resulting from elephant behaviour which, in turn, increases browsing pressure on the low-growing succulent and geophyte flora.28

The oft-repeated statement (e.g. Chown et al.27) that the persistence of the endangered flightless dung beetle (*Circeillum bacchus*) is dependent on the presence of elephants and their dung is, however, unfounded. There are populations of this species in the Gamtoos River valley and sections of the Sundays River valley (personal observation), which have not had elephants for more than 150 and 70 years, respectively.26 This is longer than the pupation period of even the most recalcitrant beetle larvae, indicating their ability to utilize non-megaherbivore dung.

Surprisingly, in the light of the history of concerns about elephant impacts in the AENP, little attention has been paid to the phenomenon of ecological cascades. Understanding these cascading effects will be critical to appreciating the influence of elephants on these landscapes.

Do elephant impacts bring about density dependence?

For more than 50 years, elephant densities in the AENP have consistently exceeded published estimates of carrying capacity (Fig. 1), and there is a well-documented decline in nutritional quality of vegetation as elephant density increases.25 The population has not been able to disperse, nor has it been subject to regulation by management. Despite this, there is no evidence of density-dependent population regulation29 through decreased fecundity or increased mortality. The population has thus been increasing very rapidly.4,29 Gough and Kerley29 hypothesized that this may be due to two factors: first, the evergreen, nutritional nature of thicket and its high standing biomass provides year-round forage; and, second, elephants have the ability to digest large volumes of low quality food, due to their large body size, and to utilize the broadest range of plants of any other herbivore in the system.11 Hence, Gough and Kerley29 postulate that the Addo elephants are buffered against a decline in nutritional resources, enabling them to degrade the landscape without showing density dependence. Other studies have shown that thicket, once severely transformed, does not achieve a stable state but continues to decline.5,12 Gough and Kerley,7 therefore, suggested that these elephants would not respond to density-dependent processes until the ecosystem is severely degraded and collapses. In this respect, the AENP elephant/thicket system appears to be analogous to Caughley’s34 non-interactive system, namely, herbivore dynamics independent of plant dynamics. However, elephants are not ‘non-interactive’ with plant production (as defined by Caughley35) as they utilize accumulated biomass rather than just annual production. Thus, once elephants deplete accumulated biomass the production base will collapse and the system will then conform to Caughley’s34 definition of an ‘interactive system’, in which herbivory has a negative feedback on herbivore populations via plant dynamics. More specifically, the interaction will conform to his ‘interferential system’, whereby co-existing herbivores will also be affected. An important consequence of this finding is that elephant demographic data cannot be used to make management decisions about elephant populations until it is too late for the plant communities and associated biodiversity.

Contribution of elephant research in the Eastern Cape to understanding elephant impacts in South Africa

A recent workshop on elephant impacts on biodiversity, hosted by South African National Parks, reviewed the available evidence in South Africa. Written submissions to this workshop focused on the effects of elephants in the Kruger National Park and the AENP. From these submissions, it is clear that despite the shortcomings in our understanding of the consequences of elephants in Addo and the methodological constraints, the findings emerging from the park are the most comprehensive and robust available. Thus, the AENP has made a disproportionate contribution to generating solutions to the elephant problem in South Africa. For example, Addo has led the way in the establishment of botanical reserves,37 which effectively conserve floristic diversity, and has been expanding elephant habitat since 1977,37 thereby reducing density. More recently, elephants have been translocated out of the AENP.29 The current review demonstrates the depth of, and highlights some of the shortcomings in, our understanding of elephant impacts. These can be used to generate biodiversity change indicators that managers can use to make decisions to intervene in elephant populations. The nature of these interventions (such as culling, contraception, metapopulation management) is currently being hotly debated at a national level.29

Discussion and conclusions

The AENP provides the best information available in South Africa on elephant impacts. This is based on more than 30 years of relatively robust science, with the botanical reserves serving as assumed controls4 for the study of the consequences of elephants. The assumption that the botanical reserves serve as appropriate controls has limited validity since the absence of elephants is as much an artefact as their presence at high densities,11,14 and it has not been possible to control for elephant density. A recent significant advance has been work using the sequential expansion of the elephant habitat in reasonably homogeneous landscapes and known elephant numbers, in order to assess impacts in terms of the cumulative density of elephants. This has the advantage of addressing both the elephant density and duration of occupation, but does, however, assume the homogeneous use of the available habitat. There is a need for studies on landscape use by elephants in order to validate this approach. The ideal research approach requires long-term surveys of a replicated series of appropriately located exclosures, which allow temporary access and monitoring of elephants so that elephant densities, duration and season of occupation can be controlled. Such a rigorous approach is especially necessary in the light of potential climate change impacts on these landscapes, and the need to distinguish between elephant and climate change effects as they are probably of the same order of magnitude and scale. Enclosures alone, however, will not provide a predictive understanding of elephant impacts, which require a greater focus on the mechanisms of the effects of elephants on biodiversity and ecosystem functioning so as to demonstrate causal relationships. As pointed out above, there is a need to develop such an understanding across the wide range of potential elephant habitat in the Eastern Cape. The recent establishment of a number of elephant populations in the Eastern Cape provides new opportunities to address this challenge.

There have been changes, ranging from soil alterations to black rhinoceros foraging opportunities, at all levels at which elephant impacts on biodiversity and ecosystem functioning have been assessed in the AENP. The clear trend is an overall decline in biodiversity. We postulate that these effects, which have been
shown on a spatially limited scale, can be extrapolated to landscape-level impacts. This review, as well as recent surveys of the effects of elephants elsewhere in Africa,\(^1\) show that the Addo represents the only current example where elephants may be driving plant species to extinction. This reflects the narrow distribution range of many thicket endemic plants\(^2\) and contrasts with the broader distributional range of most species impacted by elephants in savanna. Finally, we conclude that there is a unique urgency in understanding and dealing with the elephant problem in the Addo Elephant National Park. Short-term management measures to reduce density, such as expanding the elephant range within the park and translocation of elephants out of it, should be implemented as a matter of priority.

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