Biological Conservation 180 (2014) 122–133

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Simplification of the composition, diversity and structure of woody vegetation in a semi-arid African savanna reserve following the re-introduction of elephants

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ARTICLE INFO

Article history:
Received 10 July 2014
Received in revised form 22 September 2014
Accepted 23 September 2014

Keywords:
Colophospermum mopane
Moisture stress
Tree density
Woody structure

ABSTRACT

Elephant populations at high density commonly transform their habitat, but a low density population would not be expected to have a marked impact. Re-introduction of elephants into the Venetia-Limpopo Nature Reserve (320 km^2) in the early 1990s established a low density population for the period of survey (0.16–0.33 individuals km^{-2}). Accordingly, their impact on the composition and structure of the woody vegetation of three riparian and nine dryland vegetation types was measured between 1997 and 2010 using 148 permanent transects. Riparian habitat showed a greater change in composition and diversity, and also a greater decline of species richness, density of tall trees or total basal area, than dryland habitat. Change of dryland *Commiphora* Woodland was comparable to changes of riparian types. These conspicuous changes were a consequence primarily of severe use by elephants. Some species within these vegetation types declined markedly in abundance. Vegetation types dominated by *Colophospermum mopane* showed an increase in total basal area and relatively minor change in composition or structure, resulting mainly from the impact of moisture stress. Vegetation types that were severely impacted by elephants constituted <10% of reserve area; lightly impacted dryland *C. mopane* types constituted >70% of area. Some uncommon, selected dryland species were heavily impacted by elephants. A number of species may therefore be trending toward local extirpation. It was concluded that the coexistence of elephants and some plant species in this medium-sized, contained reserve was not possible.

1. Introduction

Persistence of elephants (*Loxodonta africana*) within sub-Saharan African is rapidly becoming centered on protected areas (Blanc et al., 2007), but this species is capable of radically transforming its habitat (Laws et al., 1975; O'Connor et al., 2007). A geographic dichotomy has developed across Africa in terms of elephant impacts. Initial concern about elephant impacts arose in the large, open-ended national parks of East Africa during the 1960s (Eltringham, 1982; Spinage, 1994, 2012), but the decimation of these populations by poaching during the 1980s allayed these concerns (Douglas-Hamilton, 1987). In contrast, the density of most southern African elephant populations, spared severe poaching impact, was controlled by management from the 1950s, after which populations have grown following reduced population control, resulting in increasing concern about vegetation impacts (e.g., Whyte et al., 2003). In addition, the growth of the tourism industry in southern Africa resulted in the re-introduction of elephants into over 58 medium-sized (<1000 km^2) to small (<200 km^2) protected areas (Garai et al., 2004). A novel challenge of managing elephants within a relatively small, closed area has therefore been created.

Current concern about elephant impacts relates not only to the effect they might have on their own population performance (e.g., Laws et al., 1975) but also their potential impact on supported animal diversity through alteration of the composition, diversity and structure of vegetation (Cumming et al., 1997; Guldemond and Van Aarde, 2008). They may also directly impact plant diversity (O'Connor et al., 2007). Elephants usually share protected areas with other large browsers or mixed feeders such as giraffe (*Giraffa camelopardalis*), kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*) and eland (*Taurotragus oryx*). Elephants may alter the availability of food resources to these species (O'Kane et al.,

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http://dx.doi.org/10.1016/j.biocon.2014.09.036
0006-3207/

2011a, 2011b) whose impact on vegetation may be as significant as that of elephants (O'Kane et al., 2012, 2013; Pellew, 1983). If management is to respond to purported elephant impacts, then it behoves scientists to ensure that impacts of other species are not falsely attributed to elephants. Furthermore, woody vegetation in African savannas is impacted by many other agents. Fire can transform savanna vegetation on its own (Trapnell, 1959) and in conjunction with elephant impacts (Buechner and Dawkins, 1961; Laws et al., 1975). Impact of stress-related agents such as drought (O'Connor, 1999) and frost (Childes and Walker, 1987; Holdo, 2006) are usually episodic in nature but can impart an indelible imprint to ecosystem organization. The significance of elephant impacts therefore needs to be judged in relation to all other potential impacts.

Elephants, like any herbivore, do not forage randomly but usually exhibit a hierarchy of selection from landscape, through vegetation type, to species and plant part (Clegg, 2010). Use of individuals of some woody species may result in their death whereas individuals of other species may maintain sound growth, depending on the manner and extent to which an individual is used (O'Connor et al., 2007). As a consequence of selection across space and differences across species in terms of impact, elephant impacts are not spatially uniform (Mosugelo et al., 2002; Vanak et al., 2012). Distribution of watering points imparts an additional spatial pattern (Chamaillé-Jammes et al., 2009; Mukwashi et al., 2012; Owen-Smith, 1996; Redfern et al., 2005; Tafangenyasha, 1997). Owing to the pronounced seasonal character of southern African savannas, elephant impacts on riparian vegetation may become pronounced during the dry season (Loarie et al., 2009). The majority of studies on elephant impacts have focused on systems in which elephants have always occurred. In the case of systems from which elephants have been absent for a number of decades, it can be expected that vegetation has altered in response to relaxation of their use. As a corollary, it should be expected that vegetation should respond to their re-introduction. Long-term study is needed to assess such responses in order that conclusions are based on vegetation that has had an opportunity to respond to a new impact through regeneration and growth.

Case studies can contribute to a deeper understanding of elephant impacts provided the similarities and differences to other cases are identified. The Venetia-Limpopo Nature Reserve (VLNR), South Africa, offered an opportunity to examine the impact of a recently re-introduced elephant population on a semi-arid savanna from which it had been effectively absent for over a century. A population of low density was established in this medium-sized (318 km^2) reserve. Animals used in the re-introduction were familiar with the vegetation as they had been sourced from areas with comparable vegetation. Fire could be excluded as a compounding factor because no fires had occurred for half a century, and all areas of the reserve were accessible to elephants owing to the density and distribution of water points. The reserve thus offered a special case of examining the impact of a low density elephant population within a medium-sized, closed system that had not been impacted by elephants for about a century.

The aim of this study was to determine whether the composition, diversity and structure of the woody vegetation of the VLNR had changed following the re-introduction of elephants. The following two hypotheses were addressed.

1. Conspicuous changes in the composition and structure of vegetation types selected by elephants would occur, of which riparian vegetation types were a prime candidate.
2. Other agents which can affect the composition or structure of woody vegetation were not expected to account for meaningful change because they have been operating within the region prior to the re-introduction of elephants.

2. Study area

The VLNR is a 31,855 ha wildlife reserve situated in the Limpopo Province of South Africa. This semi-arid region experiences a mean annual rainfall of about 366 mm (36% coefficient of variation) (31-year record) that falls during summer (November to March) (O'Connor, 1992, 1999). Annual rainfall over the period of study was highly variable (Supplementary Material 1). The first ten years of monitoring and the years preceding were generally below average with the exception of the highest rainfall season on record (1999/2000); but there was a three-year sequence of above-average rainfall from 2008 to 2010. Temperature at Musina (80 km E but comparable) ranges from 7.2 °C (June, July) to 20.3 °C (December) for average minimum monthly, and from 24.7 °C (June) to 32 °C (October, November, December) for average maximum monthly. Severe black frost is an uncommon (and unquantified) occurrence but occurred during the winter of 2010.

Topography of most of the reserve is relatively flat, on which vegetation is broadly described as Musina Mopane Bushveld, with small hills occupying about 20% of the reserve and supporting Limpopo Ridge Bushveld (Mucina and Rutherford, 2006). At a finer spatial scale, 20 main vegetation types have been described (O'Connor, 1992, unpublished). Dryland vegetation of the VLNR, which is dominated by the ubiquitous *Colophospermum mopane*, shows a close correspondence between topo-edaphic-geologic units and vegetation types (O'Connor, 1992). Geology includes base-rich, base-poor and calcium-rich rock types supporting soils with corresponding properties. A distinctive feature is a flat region underlain by deep (>3 m) palaeo-fluvial deposits of clay-loam texture occupying a third of the reserve and supporting *C. mopane* Woodland. Old crop lands are dominated by *Acacia* (now *Vachellia*) *tortilis*. (*Acacia* is retained in this paper because not all species reported on have yet been ascribed to a new genus.) Three non-perennial rivers that flow only after large storms traverse the reserve. Their associated alluvial soils that cover about 5% of the reserve support riparian vegetation types including *Acacia* Woodland on former hydromorphic grassland (MacGregor and O'Connor, 2004; O'Connor, 2001).

The VLNR was established in 1991 through the amalgamation of livestock farms. All livestock were removed at time of purchase. The population sizes for mammalian browser or mixed feeder species in 1993 was 12 for giraffe, 968 for kudu, 256 for eland, 770 for impala, and small numbers of bushbuck (*Tragelaphus scriptus*), grey duiker (*Sylvicapra grimmia*), and steenbok (*Raphicerus campestris*). Populations of kudu, eland and impala declined between 1993 and 2010; that of giraffe increased. Five black rhinoceros (*Diceros bicornis*) were re-introduced in 2004. Fire has not been an ecological factor in the VLNR since before 1950, bar a small area (<100 ha) that burnt in the north-west corner in 2002. Fourty three elephants were reintroduced into the VLNR as four separate groups between 1991 and 1994. The founder population originated from Kruger and Gona-Re-Zhou National Parks. By 2007 the founder population had increased to 68 elephants, after which 29 elephants broke into the reserve from a nearby population in Botswana in 2009. Population size was 105 elephants in 2011, occurring as seven or eight herds that merge and split frequently (Page, unpublished information).

3. Methods

3.1. Data collection

The study area was stratified first according to habitat (dryland versus riparian), and secondly according to vegetation type. A sample was drawn for the main vegetation types in which sampling