



Demography of woody species in a semi-arid African savanna reserve following the re-introduction of elephants



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ARTICLE INFO

Article history:

Received 23 August 2016

Received in revised form

29 November 2016

Accepted 31 December 2016

Available online 6 January 2017

Keywords:

Colophospermum mopane

Local extirpation

Seedling regeneration

State change

Tree mortality

Ventia-Limpopo Nature Reserve

ABSTRACT

The hypothesis that African elephants may cause the local extirpation of selected woody species was evaluated in a medium-sized, semi-arid reserve following their reintroduction at low density. Mortality, state-change, and regeneration of 25 tree and 17 shrub species were studied between 1997 and 2010. Annual mortality of shrub species ranged from 0.2 to 8.0%, with six species experiencing 6–8%. Eight shrub species lost more than half their adult population (range 10–94%). Annual tree mortality ranged from 0.2 to 10.5%. The two dominant dryland tree species experienced <1% annual mortality, 18 species lost more than half their tree population, and one was eliminated. Elephants accounted for >63% and stress-related agents >20% of tree deaths. The manner in which elephants induced tree death depended on species. The proportion of individuals of a species killed by pollarding or uprooting ranged from 0 to 74%, and by debarking from 0 to 100%. Complete uprooting was a common cause of death for three shrub species. Regeneration ranged from zero for six tree and one shrub species to a seedling every 7 m² for *Colophospermum mopane* and 23 m² for *Dichrostachys cinerea* in riparian habitat. Three shrub and eight tree species were identified as vulnerable to local extirpation owing to a combination of high mortality and poor regeneration that is likely to result in a considerably simplified system. Reintroduction of elephants into medium-sized reserves without regulation of their numbers may not be a desirable action.

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1. Introduction

Transformation of savanna woodlands by elephants (*Loxodonta africana*) has been widely reported across African parks harbouring a high density of elephants, primarily as a consequence of population compression, over the past half century (Spinage, 2012). Concern relates not only to their direct impact on vegetation (Guldmond and Van Aarde, 2007) but also to consequent effects on supported animal diversity (Herremans, 1995; Cumming et al., 1997; Fenton et al., 1998; Botes et al., 2006). In southern Africa, range for elephants has been increased through their re-introduction into a number of small (<200 km²) or medium-sized (200–1000 km²) reserves (Garai et al., 2004). Confinement of a highly mobile, large herbivore raises concern about sustainability. In one medium-sized reserve within semi-arid savanna, simplification of the composition, diversity and structure of the vegetation was observed within two decades following reintroduction of elephants at low density (O'Connor and Page, 2014), which amounted

to a change in state as described by the state-and-transition model (Westoby et al., 1989).

Two issues appear central for improving understanding of the relation between elephants and their vegetation resource. The first is why elephants choose to feed in an apparently destructive manner. The second, focus of this paper, is what determines the nature of the vegetation response. Woody vegetation of a system comprises a suite of species whose population biology can be expected to differ. Severity of elephant impact on a species population would depend on their degree of selection, manner by which a plant was used (e.g., ringbarking, removal of leaves), attributes of a plant for tolerating elephant use (e.g., bark regrowth, coppicing), and the ability for regeneration and recruitment to compensate for mortality (O'Connor et al., 2007). Local extirpation may be an extreme outcome. Elephant impact on woody plant populations may depend further on the effect of climate on population processes, habitat (Loarie et al., 2009; Pretorius et al., 2011), availability of surface water (Tafangenyasha, 1997; De Beer et al., 2006), and physical refuges (O'Connor et al., 2007).

Pursuit of a population approach for understanding vegetation response to elephant impact is, in concept, simple. Population trend

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is the net outcome of regeneration of new individuals, recruitment of different size plants, and size-dependent mortality (Harper, 1977). Elephants can potentially influence all these population processes (O'Connor et al., 2007) and change the state of a plant (e.g., tree to shrub) (Laws et al., 1975; Lewis, 1991). In practice, a number of challenges are faced. First, the lifespan of a researcher is dwarfed by the longevity of most species, which can exceed a millennium (Swart, 1963; Vogel and Fuls, 2005), yet longevity is known for only a handful of species. Second, population processes are expected to vary markedly over time on account of rainfall variability, for which cycles with a quasi-periodicity of 18 years are evident in southern Africa (Tyson and Preston-Whyte, 2000), yet studies usually endure only a few years. Third, attribution of impact to elephants must take into account concomitant impacts of other agents, including drought, fire, frost, and other herbivores. Their individual effect may match that of elephants (O'Kane et al., 2011, 2013), while their net effect may be the result of complex interactions among all agents (Pellew, 1983; Holdo, 2007; Holdo et al., 2009). Insight on the response of all species of a system is an ideal but the scale of this challenge is heightened by the relatively high species richness of African savannas (Cole, 1986).

Ostensibly as a consequence of these difficulties, detailed population studies of African woody species have been scarce (Midgley and Bond, 2001). Only a handful of studies have attempted to predict population behaviour for either a generic (Baxter and Getz, 2005) or a few species (Pellew, 1983; Wiegand et al., 1999; but see Holdo (2007) for a community-level effort), from which insights could be beguiling for anticipating elephant impacts for a relatively species-rich system.

In order to anticipate whether elephants might influence the persistence of woody species following their reintroduction into the medium-sized Venetia-Limpopo Nature Reserve (VLNR), South Africa, regeneration and mortality of all common or conspicuous woody species were studied over a period of 13 years. This amounted to 25 tree and 17 shrub species. This study focused on pattern of demographic response across species and not of detail concerning influences on the demography of individual species, which will be presented elsewhere. In order to describe the range in demographic response among species, they were compared for the following. (a) Has elephant use resulted in an increase in mortality or state-change of plants? (b) Are elephant impacts more important than those of other agents? (c) Can regeneration compensate for mortality? (d) Based on the pattern of regeneration and mortality, may some species be vulnerable to local extirpation? (e) Is the pattern of response across species consistent with this system becoming simplified (O'Connor and Page, 2014)?

2. Study area

The study was conducted on the 318 km² VLNR (22°08'–27'S; 29°13'–28'E) described in O'Connor and Page (2014). Only salient points are summarized. This semi-arid savanna receives on average 366 mm of rainfall during summer (O'Connor, 2015). Rainfall pattern over years is quasi-cyclical (Tyson and Preston-Whyte, 2000) with extended droughts. The study period from 1997 to 2010 was preceded by average or below-average rainfall, eight of the 13 years of study experienced below-average rainfall, the 1999/2000 season was the highest on record, and the final three years experienced above-average rainfall (O'Connor, 2015). Summers are hot and winters are mild. Black frost occurred during July 2010.

This study distinguishes dryland from riparian (includes riverine) vegetation. Dryland types are dominated by *Colophospermum mopane*; their species richness is related to substrate (O'Connor, 1992). Riparian vegetation is associated with non-perennial rivers and associated hydromorphic grassland

(O'Connor, 2001; MacGregor and O'Connor, 2004). Following the formation of a wildlife reserve on former ranching properties in 1991, 43 elephants were reintroduced from areas with closely similar vegetation between 1991 and 1994 that grew to a population of 105 by 2011. Thus the elephant population remained at low density (<0.15 elephants km⁻²) for the duration of the study. Over the period of survey, populations of giraffe have increased while those of kudu, eland, and impala have decreased (O'Connor, 2015; nomenclature follows Skinner and Chimimba (2005)). Small-bodied browsers are distributed throughout the reserve. No fires except one small burn have occurred since 1948 (MacGregor and O'Connor, 2002). The distribution of surface water rendered the entire reserve accessible to elephants.

3. Methods

3.1. Sampling

Following stratification of the study area according to vegetation type (O'Connor and Page, 2014), dryland and riparian habitats were sampled using 148 permanently located transects in 1997, 2002 and 2010. A transect was 50 m in length and of variable width determined by density. Transect size was then increased in order to sample additional uncommon species. Some uncommon species (e.g., *Adansonia digitata*) were also sampled off transects. A complete census of the population of *Adenia spinosa*, a semi-succulent shrub, was undertaken within its hill habitat in 1997, 2002, 2007 and 2010. The 1994 population was estimated by summing the number of live and dead individuals recorded in 1997, justified from observation that skeletons remain visible for over three years.

An individual was defined as an apparently physiologically separate unit. Most multi-stemmed individuals were easily identified or were defined based on stem aggregation and knowledge of growth habits. Each individual was identified and measured for: (i) position along the transect; (ii) stem circumference of each stem; (iii) live height; (iv) percentage loss of biomass to elephants, other browsers, stress (mainly moisture), frost, fire, or unknown. The age of lost phytomass was scored as less than (recent) or greater than 2 years (old). (v) Manner of utilisation was distinguished as branches taken, partial or complete pollarding of main stems, partial or complete uprooting, or plant death; (vi) debarking of stems was ranked as the percentage of a stem's circumference, and height, from which bark had been removed, and aged; and (vii) coppicing from stems or roots of a plant in response to damage or stress was recorded. Further detail is given in O'Connor and Page (2014). Nomenclature follows the African Plants Database (2012); *Acacia* species follow Kyalangalilwa et al. (2013).

True shrubs are defined as species which usually bear multiple stems and are not tall. A tree species possesses a limited number of stems and adults are >2 m in height; the shrub form of a tree species is ≤ 2 m in height. Regeneration is defined as an individual ≤0.2 m in height.

3.2. Mortality and state change

Mortality is defined as the absence of a previously recorded individual or of growth on a skeleton that was alive when previously surveyed. State change is defined as the loss of >50% of the previous live volume of a plant. Cause of mortality or change in state is inferred from signs on the plant guarding against false attribution to elephant for other agents whose impact may have a similar appearance. It was easy to identify mortality or state change that resulted from stress, identification of the responsible agent was context-dependent. Moisture-related stress is consistent with patterns of climatic variability and is initially apparent on a plant's

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