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Elephants and Woody Plant Diversity:

spatio-temporal dynamics of the Linyanti woodland, northern Botswana

Gabriella Teren

Abstract

There is an urgent need to study the effects of elephants on biodiversity given the ability of megaherbivores to transform vegetation composition, structure and function by killing selected plants. Within a biodiversity framework of different aspects of diversity across different scales, we need to understand elephant effects across time and space, acknowledging disequilibrium dynamics of savannas. However, most savanna studies are conducted either over a short time frame, over a limited spatial extent, or without species compositional data. The Linyanti riparian woodland in northern Botswana represents a valuable opportunity to study the effects of elephants as it is subject to extremely high elephant concentrations in the dry season as elephants congregate on the perennial river. Moreover, because of trampling effects by large herbivores and high soil moisture, fire is largely excluded, allowing the study of intense elephant impacts in relative isolation.

This PhD thesis aims to assess long-term (16-18 years) compositional and structural change at a large spatial scale (50 km of riverfront) of the Linyanti riparian woodland, built upon two earlier studies in 1992/2 and 2001. Specifically, it aims to establish the effects of elephants on 1) the spatial heterogeneity of disturbance across the woodland; 2) compositional changes of the canopy tree layer caused by elephant impacts; 3) the potential of the woodland to regenerate from seedlings; 4) structural changes due to woodland decline and shrub increase. It finally aims to synthesise these findings for biodiversity and the implications for conservation and management.

Spatial heterogeneity was assessed by delineating patches of intense disturbance using the clustering algorithm DBSCAN. I manually marked dead trees within a 2000 ha overlapping riparian area from the 1992, 2001, and 2010 aerial photographs and determined these trees were significantly clustered in the landscape to form patches of disturbance. Disturbance patches were highly dynamic over the period where small patches appeared, grew and coalesced over time, whilst a few patches fragmented or disappeared. The overall dynamic was of smaller patches coalescing resulting in the total patch area increasing from 6% in 1992 to 23% in 2010. Mortality increased mostly in the inter-patch areas but the overall dead tree appearance rate of 0.28 trees.ha.yr^{-1} was not much higher than a background tree

death rate calculated for exclosures in other areas. The slow mortality rate coupled with progressive decline suggests there was little recruitment into the canopy to replace the trees that were lost. Even though large areas remained that were not classified as disturbance patches, there was evidence of increased fragmentation where inter-patch areas became increasingly small and isolated. This increase in greater areas of disturbance represents a state shift to decreased heterogeneity although landscape patchiness still remained in 2010. Projections were that mortality rate and patch formation would decrease.

To assess compositional changes, I reconstructed the pre-1992 canopy tree woodland by combining both living and dead trees in 1992, and compared this to the 1992 and 2008 woodland composition. The woodland showed progressive declines from an *Acacia* spp.-*Colophospermum mopane* dominated tall tree woodland pre-1992 to a woodland in 2008 composed primarily of two resilient species (*C. mopane, Combretum hereroense*), and one avoided species (*Philenoptera violacea*). I compiled Size Class Distributions of individual canopy tree species and compared proportional high impact on living and dead trees between 1992 and 2008. High elephant impact was defined as more than 50% stem circumference ringbarked or with the main stem or majority of side stems broken. I found that elephant impact was the likely cause of the woodland decline, although wind and natural senescence were variably important for some species. The acacias had nearly disappeared from the woodland, declining in proportional abundance from 30% in the reconstructed pre-1992 woodland to just 4% in 2008. Over time there was a progressive shift in elephant impact from abundant preferred and vulnerable species like *Acacia* spp. and *Terminalia* spp. to species more resistant to debarking like *Combretum imberbe* and *Berchemia discolor*. The abundant species *C. mopane* proved highly resilient to intensive elephant impact. The seedling layer (plants below 0.5m) had high proportions of canopy tree species including the acacias, and all but the rarest species were recorded. This suggests regeneration of the woodland is possible but there was a demographic bottleneck of seedling mortality with few saplings recorded over the time period.

To determine the structural changes which have taken place, I separated shrub species and canopy-forming tree species and assessed density changes in the sapling (<2.5m) and tree (>2.5m) layers. Tall (>2.5m) canopy tree density decreased by half between 1992 and 2008, representing an annual loss rate of 2.7% without replacement. Except for *Colophospermum mopane*, there was no compensatory regeneration in the form of saplings. *Colophospermum mopane* was highly resilient to elephant impacts, coppicing vigorously following impact to form local 'browsing lawns' which may benefit other browsers. The overall shrub density increased 2.5 times while one shrub species (*Combretum mossambicense*) increased five-fold in density and came to constitute 50% of the total woody plant density. This shrub species increased rapidly, at an exponential growth rate of 10.5% per year,

representing pervasive shrub encroachment. Its invasion wave was incipient in 1992 and by 2008 many of these plants had grown beyond 2.5 m in height, forming a dense screen. Small plants of this species <1 m in height had become sparse by 2008, suggesting that the invasion had become curtailed by then. I proposed that the spread of this shrub was due to its unpalatability by elephants, although it is an important browse species for ruminants. A potential global driver of enriched atmospheric CO_2 or regional aridification could not be ruled out. The state shift from woodland towards dense shrubland caused by differential elephant impacts has potential negative consequences for structural and functional diversity.

I attempted to synthesize the findings for biodiversity and concluded that there was a state shift towards pervasive disturbance with a corresponding decline in spatial heterogeneity, although composition of the disturbance patches was not studied. There has however, not been a state transformation from woodland and stands of tall trees were still present in the woodland. Coupled with the potential regeneration of the woodland from seedlings, these findings highlight the importance of long-term studies of non-equilibrium savannas. The main threat to biodiversity of the woodland was not elephant-induced mortality of large trees, but rather the lack of recruitment and the pervasive shrub encroachment of a single species. It may be, however, that alternate states of canopy trees and unpalatable shrubs exists, enhancing long-term functional diversity, provided the system remains relatively open and elephants are free to move to other areas. Ultimately the only management strategy of relatively open areas with high elephant concentrations is to accept changes and support transfrontier conservation efforts. I further assess the limitations of this study, and make recommendations for future study, specifically highlighting the need for a longer-term palaeo-ecological study to evaluate compositional changes due to episodic recruitment events.