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# Decomposition rates of organic material across herbivore treatments in a nutrient-rich semi-arid sodic savanna

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# Abstract

Decomposition is a major determinant of terrestrial nutrient cycling and therefore an important regulator of ecosystem structure and function. It has been widely documented that large mammalian herbivores (LMH) act as a significant driver of changes to above ground structure and modifications to edaphic properties. Little is known about the role of herbivory, and particularly the loss thereof, in mediating essential ecological processes in a herbivore-adapted system. The Nkuhlu exclosures, a large-scale, long-term exclusion experiment in the Kruger National Park, South Africa, provided an opportunity to explore the effects of herbivory and/or its long-term exclusion on decomposition and stabilisation of detrital plant material. An extended, site-specific version of the Tea Bag Index approach was used to quantify decomposition rate (k) and stabilisation factor (S) of standardised litter substrate. Two hundred and fifty tea bags (125 green and 125 rooibos tea bags) applied in a paired tea bag design were exposed to three herbivore treatments along the sodic zone of the Nkuhlu exclosures and removed after three months of incubation. Decomposition rates (k) were highest in the presence of LMH and lowest in their absence. Conversely, stabilisation factor (S) was significantly higher in treatments from which herbivores have been excluded for ~18 years. Our study provides evidence that LMH can influence essential ecological processes such as decomposition and stabilisation of detrital plant material. Moreover, results confirmed that ecosystems that evolved with herbivores, are sensitive to herbivore loss as it reduces decomposition rates of plant detritus and hence, decelerates ecosystem nutrient cycling.

# Introduction

Savannas are dynamic systems with a high degree of complexity, mainly due to their spatial heterogeneity – the product of system-specific drivers (Grant and Scholes, 2006; Van Coller *et al.*, 2013; Wigley *et al.*, 2020). Savannas are faced with numerous challenges, including heavy utilisation pressure from single-species domestic livestock at the expense of heterogeneous savanna herbivore communities, which contribute towards the structural and functional degradation of these systems (Grant and Scholes, 2006; Van Coller *et al.*, 2013; Eldridge *et al.*, 2019; Tuomi *et al.*, 2019; Wigley *et al.*, 2020). Herbivory is an agent of disturbance and functions as one of the primary drivers of system dynamics in African savannas (Grant and Scholes, 2006; Van Coller *et al.*, 2013). Numerous studies have reported on the ability of large mammalian herbivores (LMH) to alter vegetation structure and edaphic properties of a system (Grant and Scholes, 2006; Van Coller *et al.*, 2013; Eldridge *et al.*, 2019; Wigley *et al.*, 2020). Changes to system structure have the potential to directly influence and alter soil function in terms of decomposition and stabilisation of detrital plant material (Keuskamp *et al.*, 2013; Becker and Kuzyakov, 2018; Eldridge *et al.*, 2019; Tuomi *et al.*, 2019; Wigley *et al.*, 2018; Eldridge *et al.*, 2019; Wigley *et al.*, 2019; Wigley *et al.*, 2018; Eldridge *et al.*, 2019; Wigley *et al.*, 2019; Wigley *et al.*, 2018; Eldridge *et al.*, 2019; Wigley *et al.*, 2019; Wigley *et al.*, 2018; Eldridge *et al.*, 2019; Wigley *et al.*, 2019; Wigley *et al.*, 2018; Eldridge *et al.*, 2019; Wigley *et al.*, 2020)

In southern African savannas, edaphic properties are stronger determinants of intensively utilised patches (IUP) than animal biomass alone (Grant and Scholes, 2006; Van Coller *et al.*, 2013). Sodic patches are prominent IUP's in granitic landscapes that are structurally open areas, which improve predator vigilance (Van Coller *et al.*, 2013). LMH are also responsible for the formation and the maintenance of wallowing points in these systems during the wet season (Grant & Scholes, 2006; Van Coller *et al.*, 2013). Sodic patches are ecologically important as they provide a positive nutrient feedback loop promoted by congregated herbivore activity (Grant and Scholes, 2006; Van Coller *et al.*, 2013). Herbivores are therefore responsible for maintaining invaluable ecological processes and corresponding integrity of sodic systems.

Large parts of protected African savannas are faced with herbivore loss, albeit the diverse suite of LMH, or elephants only (Van Coller *et al.*, 2013; Wigley *et al.*, 2020). Such losses might affect several underlying processes including soil-based decomposition and stabilisation of detrital plant material (Becker and Kuzyakov, 2018; Eldridge *et al.*, 2019; Tuomi *et al.*, 2019; Wigley *et al.*, 2020). Decomposition entails the biochemical-driven degradation of complex organic compounds through mainly, microbial-mediated processes (Keuskamp *et al.*, 2013; Eldridge *et al.*, 2019; Petraglia *et al.*, 2019). Decomposition studies are

covered extensively for temperate and boreal ecosystems, while studies in subtropical ecosystems, especially in Africa, remain limited (Becker and Kuzyakov, 2018; Erasmus *et al.*, 2021).

Despite extensive use of exclosure experiments to investigate herbivore impacts, there is little consensus on their direct and indirect effects on soil function, particularly on decomposition and inherently, above– and belowground carbon sequestration (Eldridge *et al.*, 2019; Tuomi *et al.*, 2019; Wigley *et al.*, 2020). The Nkuhlu exclosures located within the Kruger National Park (KNP) provided an opportunity to examine the potential influence of complete (all LMH) or partial (only elephants) herbivore loss on essential ecological processes. This study therefore aimed to assess the intrinsic role of herbivores in soil-based decomposition and stabilisation in a herbivore-adapted semi-arid, sodic African savanna. We hypothesised that the decomposition rate and stabilisation factor of organic material would differ across different herbivore treatments as herbivores actively alter key regulatory constituents of the decomposition subsystem. To test this hypothesis, we applied the Tea Bag Index (TBI) approach across three herbivore treatments with varying intensity to determine the effect of herbivory on potential soil-based decomposition rate (*k*) and stabilisation factor (*S*) of detrital plant material through the quantification of standardised litter.

### Methods and Study Site

The study was conducted in the semi-arid Dry Sodic Savanna of the Nkuhlu research site (24°58'S, 31°46'E) located on the northern bank of the perennial Sabie River approximately 18 km downstream of Skukuza in the KNP, South Africa (Siebert and Eckhardt, 2008). Situated beneath the seepline on the foot slopes of undulating granitic landscapes ranging between 200 and 230 m above sea level (a.s.l.), the study site is characterised by sodium-rich, deep duplex soil, referred to as the sodic zone (Siebert and Eckhardt, 2008). The Nkuhlu exclosures were constructed in 2001 as part of a large-scale, long-term exclusion experiment based on the removal of certain ecosystem drivers (e.g. herbivory and fire) (Siebert and Eckhardt, 2008). Herbivores have therefore been excluded for 18 years at the time of data sampling for this particular study. The experimental site is divided into three herbivory treatments comprising of (1) a partially fenced area (Elephant exclosure) designed to exclude elephants based on body size (also excluding giraffes), (2) an unfenced area (Control) which allows for unrestricted movement of all LMH and (3) a fully fenced area (LMH exclosure) excluding all herbivores larger than a hare (Siebert and Eckhardt, 2008).

The TBI approach introduced by Keuskamp *et al.* (2013) is an internationally standardised, user-friendly method to collect comparable, globally distributed decomposition data. Test kits comprise of commercially available tea bags (Lipton® rooibos and green tea). Standardised litter (tea leaves) enables the TBI to identify and examine environmental drivers of decomposition without the ambiguous effects of site-specific litter, serving as a reference which facilitates data comparison across spatial scales (Keuskamp *et al.*, 2013; Becker & Kuzyakov, 2018; Petraglia *et al.*, 2019; Erasmus *et al.*, 2021). The TBI comprises of two parameters describing (1) decomposition rate (k-rate at which detrital plant material is lost) and (2) stabilisation factor (S-sequestration of detrital plant material). Methodology conformed to the extended, site-specific version of the TBI approach as described in Teatime in Kruger (Erasmus *et al.*, 2021). Tea bags (125 green and 125 rooibos tea bags) were buried at a depth of 8 cm in a paired design among the three herbivore treatments in a sodic savanna ecosystem. After a three-month incubation period, tea bags were retrieved, followed by the standard protocol to calculate k- and S-values as described in Keuskamp *et al.* (2013). Results were compared with TBI values obtained from a diverse range of ecosystems globally (Figure 1).

Since the data did not meet assumptions of normality according Kolmogorov–Smirnov and Shapiro–Wilk normality tests, a Kruskal-Wallis ANOVA was applied to the data in Statistica, (V13.3, TIBCO Software Inc., 2017) to test for significant variation in k and S of standardised litter amongst three herbivore treatments. Where statistically significant variance among treatments were attained, multiple comparisons of mean ranks were applied as post-hoc tests. Significance levels for all analyses were set at the standard significance level (p < 0.05) enabling confident conclusions made from statistical results.

#### Results

All measured k- and S-values occupied a similar range as that of global TBI references derived from Keuskamp *et al.* (2013) and Becker and Kuzyakov (2018). System 15 (Tanzania, savanna –Figure 1) is the only system that partially relates to the study area in terms of system structure (Siebert & Eckhardt, 2008; Becker & Kuzyakov, 2018). Obtained S-values from the study area differs substantially from that of system 15, whereas k-values are more related (Figure 1). This supports the notion that S is dependent on environmental and climatic factors, reflecting site-specific drivers (Keuskamp *et al.*, 2013; Becker & Kuzyakov, 2018).



LMH exclosure, all LMH excluded; Elephant exclosure, elephants (and giraffes) excluded; Control, all herbivores present.

**Figure 1:** Mean decomposition rate (k) and stabilisation factor (S) within a subtropical, semi-arid southern African savanna at the Nkuhlu exclosures, Kruger National Park. This system is divided into 3 herbivore treatments (coloured circles). Whiskers indicate standard error of the mean based on the results obtained from 250 tea bags (125 green & 125 rooibos) over a 3-month incubation period. Black dots represent global TBI references adapted from Keuskamp *et al.* (2013) and Becker and Kuzyakov (2018).

Mean decomposition rate (k) decreased with increasing stabilisation factor (S) which corresponded with a release in herbivory pressure (Figure 2). After a 3-month incubation period, k of standardised litter did not vary significantly across herbivore treatments (p > 0.05; Figure 2a), whereas S varied significantly across treatments (p < 0.05; Figure 2b). S was significantly higher in the LMH exclosure when compared to the control (multiple comparisons: p < 0.05; Figure 2b), which corresponds with the lowest k-value in this treatment (Figure 2a).



LMH exclosure, all LMH excluded; Elephant exclosure, elephants (and giraffes) excluded; Control, all herbivores present;  $\pm 1.96^*$ , standard deviations of the mean; SE, standard error; p, p < 0.05 indicates a significant differences between groups.

**Figure 2:** Mean decomposition rate -*k* (a) and stabilisation factor -*S* (b) of standardised litter after a 3-month incubation period across three herbivore treatments within the Nkuhlu exclosures, Kruger National Park. Significant differences (p < 0.05) between herbivore treatments are indicated with different lowercase letters.

#### Discussion

Obtained results varied substantially from other systems (Figure 1), echoing the unique ensemble of environmental drivers present within the studied system. Differences between k- and S-values from the studied system and its closest relative (system 15 - Tanzanian savanna, 951 m a.s.l.) may be ascribed to combined effects of elevation and climatic variation on soil processes (Becker & Kuzyakov, 2018). Systems situated at low elevation, especially in semi-arid environments (such as the study area) are highly subjected to climatic limitations (temperature and moisture) which directly influence decomposition (Grant & Scholes, 2006; Becker & Kuzyakov, 2018). Higher decomposition rates (k) in the presence of all LMH (control) can be ascribed to the ability of LMH to alter vegetation structure and edaphic properties, specifically to enhance

decomposition factors (Grant and Scholes, 2006; Semmartin et al., 2008; Van Coller et al., 2013; Eldridge et al., 2019). High intensity utilisation of savanna vegetation results in decreased carbon-based secondary metabolites (recalcitrant compounds such as tannins and polyphenols), decreased C:N ratios and increased nutrient content within vegetation tissue, rendering highly utilized vegetation more palatable, nutrient-rich and labile (Grant and Scholes, 2006; Siebert & Eckhardt, 2008; Van Coller et al., 2013). LMH influence patchspecific soil nitrogen (N) availability through excretions (i.e. urination and defecation) which stimulate microbial metabolic activity and subsequent decomposition of detrital plant material (Grant and Scholes, 2006; Semmartin et al., 2008; Eldridge et al., 2019). System perturbation, which may be associated with high LMH activity, correlate with decreased stabilisation and a subsequent decrease in soil organic matter (SOM), which result in increased microbial demand for organic carbon and subsequently, a more rapid detrital turn-over (decomposition) (Semmartin et al., 2008; Becker and Kuzyakov, 2018; Eldridge et al., 2019; Petraglia et al., 2019). Increased SOM due to high stabilisation (significantly higher S in the LMH exclosure) results in fertile soil with a higher productivity potential (biomass production). Several studies have indicated that absence of herbivores lead to increased standing biomass (Grant and Scholes, 2006; Van Coller et al, 2013). Low soil temperatures associated with the shading effect of high biomass can promote stabilisation as it results in reduced microbial metabolic activity (Keuskamp et al., 2013; Becker and Kuzyakov, 2018; Eldridge et al., 2019; Petraglia et al., 2019). Ungrazed grass often becomes moribund, reducing the amount of plant material that enters the decomposition subsystem. Nutrients are locked up in the aboveground compartment rendering them unavailable, negatively influencing soil-based microbial abundance and activity. This effect is evident from the results as S of standardised litter increased with a decrease in herbivore pressure. Moreover, the study area is situated within a moisture-limited system (561 mm per year) further impeding microbial activity and subsequent decomposition (Grant & Scholes, 2006; Keuskamp et al., 2013; Becker and Kuzyakov, 2018; Petraglia et al., 2019).

Decomposition functions as a bottom-up system control and is a major determinant of system dynamics. Yet, little is known about site-specific disturbance effects such as herbivory or the loss thereof on essential ecological processes. Decomposition and associated carbon flux studies are covered extensively in the northern hemisphere, while studies in African systems remain limited. TBI-based decomposition studies provide a relatively easy approach to obtain valuable information regarding system disturbances and their potential effect on ecosystem functioning. Studies aimed at elucidating decomposition dynamics and the role of various influencing factors such as herbivory is essential to better understand and effectively manage soil function together with associated carbon cycling.

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