CHARACTERIZATION OF BIOTIC AND SODIC LAWNS OF THE KRUGER NATIONAL PARK USING THE FRAMEWORK OF THE POSITIVE FEEDBACK LOOP

by

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Abstract

The classical grazing lawn model is an intensely-grazed patch composed of short-statured, grazing-tolerant grass species. The formation and maintenance of these communities is controlled by positive feedbacks between grazers and the high-quality resource forage that the component grass species provide. Different nutrient cycling dynamics among the lawns identifies two discrete lawn types in the savanna: biotically-driven lawns on nutrient-rich gabbroic soils and abiotically-driven lawns at sodic sites. We were interested in identifying whether the biotic and sodic lawns represented two distinct systems in terms of the feedback responses among herbivores, decomposers and grass and decomposer community assemblages in a mesic savanna. We sampled these components of the abiotic and biotic template of five sodic and five biotic lawns in the Kruger National Park. We used β diversity in grass and dung beetle community assemblages among the lawns to identify whether sodic and biotic lawns were distinct for grass percent cover and dung beetle species abundance. Four and three categories of lawns were identified for these traits, respectively, and placed the lawns on a gradient from biotic-like to sodic-like with a range of intermediates. Soil Na content was higher among sodic lawns but these levels did not manifest themselves in the grass foliar Na content, as for biotic lawns. Herbivore utilization of the sodic lawns was higher than the biotic lawns. Biotic lawns showed no difference in herbivore metabolic biomass between the late-wet and early-mid dry season. We concluded that the systems of nutrient cycling and lawn maintenance are distinct between the biotic and sodic lawns, but that the lawns exist along a gradient in terms of their community characteristics and abiotic features. Efforts to classify grazing lawns will present benefits in improving our understanding of their dynamics and, resultantly, the management and conservation approaches that use them to control herbivore populations in African savanna ecosystems.

Introduction

Intensely grazed patches of short-statured, mat-forming grass species are a historical and important component of many savanna ecosystems in Africa (McNaughton 19894; Archibald 2008; Cromsigt & Olff 2008; Stock *et al*. 2010). These patches support grazing-tolerant grass species that are more productive and palatable than surrounding tall, bunch grass assemblages (Cromsigt & Olff 2008; Coetsee *et al*. 2010b). This high quality forage concentrates herbivores in the area, promoting frequent and intense grazing that leads to a shift in grass community structure from caespitose, upright species to short, grazing-tolerant species (Archibald 2008; Cromsigt & Olff 2008; Coetsee *et al*. 2010b; Stock *et al*. 2010). These lawn-forming grasses display traits that reflect their coevolution with grazers, including vegetative, lateral spreading via stolons and rhizomes, and the production of low-lying but high bulk forage biomass (McNaughton 1984; Agrawal 2000; Agrawal 2004; Cromsigt & Olff 2008; Coetsee *et al*. 2010b).

Accelerated primary production of the grass is also linked to enhanced quality of the forage resource as the foliage is maintained in a phenologically young, nutritious and palatable stage under heavy grazing pressure (McNaughton 1984; Archibald 2008; Cromsigt & Olff 2008; Coetsee *et al*. 2010b). In this way, grazers have an effect on the nutrient cycle dynamics of the patches as the grasses increase the efficiency of nutrient uptake from the soil to enhance allocation, of N in particular, to their shoots (Coetsee *et al*. 2010b; Stock *et al*. 2010). This high nutrient output requires enhanced rates of cycling from litter inputs, such as dung and urine, and productive decomposer communities to maintain soil nutrient stocks and the sustainability of the ecosystem (McNaughton 1984; Coetsee *et al*. 2008; Stock *et al*. 2010). This suggests a biotic turnover model where soil nutrient status, grass species composition, herbivore utilization rates and decomposer community composition interact to maintain the lawns. On these biotic lawns, the increased nutrient input from grazers allows the lawn grasses to display compensatory growth required to prevent invasion and shading out by bunch grasses (Cromsigt & Olff 2008). This feedback model is described among classical grazing lawns in East Africa (McNaughton 1984; Grant & Scholes 2006).

However, the biotic component is not always the key driver in nutrient cycling on lawn patches (Grant & Scholes 2006). In some cases, herbivores and decomposers do not contribute to nutrient turnover because the soil of the lawn patches is already nutrient enriched (Grant & Scholes 2006). This deviation from the biotic model suggests that these lawns withstand the intense grazing required for lawn maintenance through abiotic means. In addition, the nutrient cycling will also be more susceptible to abiotic variables, including rainfall, runoff and evapo-transpiration (Khomo & Rogers 2005). Patches with short, grazing-tolerant grasses that occur in areas of hyper-accumulation of clay and sodium at catenal footslopes (Khomo & Rogers 2005) are examples of abiotically-driven lawn systems. These sodic sites are highly attractive to grazers and support an unusually high abundance of herbivores which take advantage of both the nutritious foliage and accumulated salts through mineral licks to satisfy mineral deficiencies in their diets (McNaughton 1988). The importance of grazers on these sodic lawns is revealed through exclosure experiments which suggest that herbivory is still required for their maintenance as grazing-tolerant short grass patches (van Coller *et al*. 2013).

On both biotically- and abiotically-driven lawns (hereafter referred to as "biotic" and "sodic" lawns) in mesic savanna, grazers obtain their metabolic requirements from productive grasses during the wet and early dry seasons. On both lawn types, therefore, short grass community structure is maintained through positive feedback with grazers (Archibald 2008; Coestsee *et al*. 2010). However, biotic and sodic lawns differ in the nutrient cycling dynamics that maintain the grass community after defoliation. Despite this intrinsic difference between biotic and sodic lawns in their nutrient dynamics, they both fall within the general framework of the originally described "grazing lawn" system that requires and has adapted its grass community to intense, persistent grazing (Olivier & Laurie 1974; McNaughton 1984). While biotic and sodic lawns appear to represent contrasting lawn types within this framework, there is high variability within each type that suggests overlap in characteristics between them. Khomo and Rogers (2005) observe the great variability among sodic lawns in the Kruger National Park from lawns with sparse vegetation to those displaying complete denudation. Similarly, biotic lawns are also likely to display great variability in composition, structure and control dynamics due to the interplay between bottom-up and top-down factors that influence them. As a result, biotic and abiotic characteristics are expected to place lawns identified as "biotic" and "sodic" on a gradient rather than on opposite, distinct ends of the grazing lawn framework.

In the Kruger National Park, we were interested in identifying whether this difference in the two lawn types makes them two distinct lawn types in the savanna landscape. This question was addressed by placing both lawn types on the framework of the positive feedback loop between the biotic components, namely grass, herbivore and decomposer communities, and abiotic components, including soil quality. We first investigated whether grass community assemblages clearly define the distinct *a priori* biotic and sodic lawns or whether this trait identifies mixed lawn types within these two lawn types. Secondly, we explored soil and foliar nutrient status and were interested in identifying whether these traits are associated with each other and determine different herbivore foraging patterns between the lawns. The difference in herbivore utilization patterns with season was also be investigated between the biotic and sodic lawns. Finally, dung beetle community structure and composition was investigated to establish whether decomposer assemblages differ between the lawns or, again, whether intermediate lawn types are artificially assigned to the biotic and sodic categories due to their existence along a decomposer community gradient. Whether nutrient turnover requires decomposers on both lawn types was also addressed, as well as the variability in decomposer community structure with vegetation or soil type. Questions addressing community assemblages will adopt a measure of β diversity as a quantitative tool for comparison between sodic and biotic lawns. The study is aimed at testing the hypotheses that biotic lawns are separate lawn patch systems from sodic lawns, and that feedback with biotic components of the system is more important for the persistence of the biotic than the abiotic lawns. We predict that by addressing this question, we will also confirm that the dichotomous classification of lawns as biotic and sodic is false and that large variation among lawns on all levels of the positive feedback loop places them on a gradient of community characteristics.

Methods and Materials

Study area

Grazing-tolerant short grass patches, referred to as grazing lawns, were sampled between the Phabeni gate and Skukuza in the south-western region of the Kruger National Park (KNP), South Africa (24. 98° S 31.60° E). This region of KNP is characteristically mesic savanna with an annual average rainfall of 547 mm and maximum rainfall during the summer months between October and April (Venter *et al*. 2003). The region is gently undulating with an underlying geology of Archaean granites and sill intrusions of Timbavati Gabbro (Schutte 1986; Walraven 1986; Scholes *et al*. 2001). Coarse-grained, clayey soils at the footslopes of the catena are deep (> 100 cm) and nutrient-rich due to accumulation of leached cations, especially Na (Venter 1986; Scholes *et al.* 2001; Grant & Scholes 2006). The Timbavati Gabbros form younger sandy-clay soils on the catena uplands (Schutte 1986; Scholes 1990; Venter *et al*. 2003). Vegetation of the area is mixed lowveld bushveld with dense grass communities interspersed with broad-leaved woody species, including *Acacia gerrardi* and *Euclea divinorum* (Scholes *et al*. 2001; Venter *et al*. 2003; Grant & Scholes 2006). The landscape supports a diverse suite of ungulates and megaherbivores, including impala, rhino and hippo throughout the year (Scholes 1990).

Sampling strategy

Two sets of ten lawns were sampled at different sites in the study region and at different times between 2012 and 2013. The first set of lawns was sampled between 25 - 27 February, 2012 (“2012” lawn set). The second set of lawns was sampled during 2013 on two different occasions: 1) 9 – 14 February 2) 6 – 8 May (“2013” lawn set) (Appendix 1). Five of the lawns in each set were sampled at sodic sites (S1 – S5) at catenal footslopes. Sodic lawns were identified by sparse vegetation and hard, calcareous soil surfaces that were pale in colour. Biotic lawns (B1-B5) were sampled on the gabbroic soils of the catena uplands and identified by the presence of low-lying grass species. Lawns sampled on the same soil type within each set were approximately 100 m from each other and lawn boundaries were identified by the presence of tall bunch grass species.

Grass community assemblages

The grass community assemblages on the 2012 lawn set were recorded by Bijl *et al*. (2012). Within ten randomly distributed 1m^2 quadrats on each lawn, all grass species were identified and the percent cover of each was estimated. The ten observations were then used to obtain average percent cover per species for every lawn. The grasses were identified to species level where possible, and assigned to one of the following growth form categories: 1) mat-forming or 2) bunched, tussock-forming, according to Stock *et al*. (2010) and Gulzar *et al*. (2012).

Soil nutrient status

We collected five soil samples from the upper 30 cm of the soil at randomly selected points on each biotic and sodic lawn of the 2013 set. Five randomly distributed samples were also taken in the surrounding tall grass areas of each lawn, resulting in 100 samples. Samples on sodic lawns included both the hard upper clay layer (average depth = 9 cm) and the soil below this level. We collected the soil samples in brown paper bags, air dried them over 3 days and sieved them through a 2-mm sieve to remove organic matter. We then weighed out 10g of each sample and prepared them for pH and EC analysis according to Alban and Kellogg (1959). We measured pH and electric conductivity (EC) of each sample using a HANNA HI-9321 pH meter (calibrated using pH 4.1 and 7.0 KCl solutions) and a HANNA HI-98188 conductivity meter (NaCl calibrated), respectively. 10g of each soil sample was also sent for analysis of extractable concentrations of K, Mg, Na and P at the Elsenburg Plant Production laboratory (Stellenbosch, South Africa).

Grass nutrient status

On each lawn of the 2013 set, we identified grasses to species level where possible and estimated the relative cover of each species by visual inspection. Grasses that were dominant on each lawn (>50% of total lawn grass cover) were selected for sampling. *Sporobilus ioclados* was the dominant species on all sodic lawns, while *Digitaria aerianthus* was dominant on B1, B3 and B4 and *Bothriochloa* sp. and *Themeda triandra* were dominant on B2 and B5, respectively. We collected green foliar tissue of these species to yield a sample of 5g (dry mass). Samples were dried at 60 °C for 24 hours, finely ground using a rotary hammer mill and analysed for total C, NH_4^+, K, Mg, Fe and Na content at Elsenburg Plant Production laboratory.

Herbivore presence and utilization

Dung counts and bite marks

Dung counts were used as a long-term indicator of herbivore presence on the 2013 set of lawns in February (data from Chan *et al*. 2013). The abundance and species identity of dung was recorded within nine $1m^2$ quadrats on a 20m transect along the centre of biotic lawns and 15 quadrats on a 50m transect on the sodic lawns. Sampling was shifted 1m down the transect when large rocks or no vegetation cover was observed in the quadrat. All dung events were included in the survey regardless of age and scattering. We used average biomasses of both males and females of each species, obtained from literature on African savanna fauna (Cumming & Cumming 2003; Stock *et al*. 2010) (Appendix 3), and total species abundances to determine the metabolic biomass of each species, according to Kleiber (1975).

Bite marks were also visually surveyed along the transects as a proxy for herbivore utilization of the lawns. The percentage of grass blades that were bitten was estimated and used to assign each quadrat to one of the following utilization intervals: 0%, 0-1%, 1-3%, 3-12%, 12-25%, 25-50%, 50-75% and 75-100%. Using the midpoints of these intervals, we then determined the average utilization (± se) of each lawn.

Camera trapping

We conducted three camera-trap surveys of grazers and mixed feeders on the 2013 lawn set using passive, infrared Bushnell cameras. We set up traps at two different times in 2013: 1) five days in February (107 ± 3.60 hours) (late wet season) (data from Chan *et al*. 2013) 2) 1 -10 days in May (29.44 ± 2.74 hours) (early-mid dry season). We programmed the cameras to record a video for 30 seconds, followed by a five-minute delay (February) or take a photograph (May) when triggered by motion. Cameras taking photographs also took pictures at five-minute intervals without being triggered by motion. The cameras were secured to trees at each lawn so that the maximum amount of lawn area was in each camera's field of view and set to run for 24 hours/day.

We analyzed the photos and videos for species identification of grazers and mixed feeders and recorded their abundances at each independent trapping event. Events were considered independent if one or both of the following criteria were met: 1) consecutive photos/videos of conspecific individuals taken > 30 minutes apart 2) non-consecutive photos of conspecific individuals (Rovero & Marshall 2009; Negroes *et al*. 2010). In cases where abundances within a herd differed between consecutive photos/videos recorded in an independent event, the average abundance across the recordings was taken as the herd abundance for that event. We then totalled abundances within species for each lawn and determined the total metabolic biomass for each species on each lawn, as above.

To account for uneven sampling effort within the May trapping period, we only analyzed independent events on each lawn that took place within the time interval defined by the camera that ran for the shortest time in each trapping period. Data from May traps is therefore obtained from approximately 1 day (29.44 ± 2.74 hours) of trapping. To determine the total time of sampling (after excluding data after the 1st day), the time at the end of trapping was recorded as that of the last recorded event on the last day of trapping. Total species biomass and total trapping time were then used to calculate total metabolic biomass/hour for each species on each lawn. We also totalled metabolic biomass/hour across all species to obtain an overall value for each lawn.

Dung beetle community assemblages

We sampled dung beetle communities on the lawns of the 2013 set using three baited pitfall traps on each lawn. We constructed the traps using 3ℓ plastic buckets with a diameter of 170 mm and filled each with 5 cm of water and soap to reduce water surface tension. The traps were set into holes in the ground at distances of 6m from each other in a triangular formation at the centre of each lawn. We avoided setting traps up in proximity to woody vegetation which could have influenced dung beetle flight patterns and other activity. We placed elephant dung in mesh bags on top of a cross-hair constructed from wire across the trap opening as bait for generalist dung beetles. Traps were left for 24 hours and then sampled by collecting all dung beetles in brown paper bags. The set-up procedure was then repeated and the traps were left for another 24 hours before re-sampling. Dung beetles were identified to genus level, where possible, or classified into morphospecies.

Statistical analysis

Grass community assemblages

We combined quadrat-level percent cover to provide single measures of cover for each species at the lawn level. We then quantified the β diversity in grass community composition by calculating pairwise distances between all lawns using the Bray-Curtis index of dissimilarity (Koleff *et al*. 2003; Anderson *et al*. 2010). β diversity of grass percent cover is a measure of community variance, or turnover between sample units (lawns) that do not exist on an environmental gradient (Anderson *et al*. 2010). We chose the Bray-Curtis distance measure because it includes relative abundance information in the data and it does not assume that joint absence of a species between lawns increases their similarity (McArdle and Anderson 2001; Anderson *et al*. 2006; Legendre & De Caceres 2013).

We then used the distance measures to identify whether β diversity in grass species percent cover is distinct between the *a priori* biotic and sodic lawn groups identified in this study. This was performed using a permutational multivariate dispersion analysis (PERMANOVA), which is a non-parametric, multivariate analogue of the Levene's test of homogeneity (McArdle and Anderson 2001; Terlizzi *et al.* 2005; Anderson

2006; Ricotto and Burrascano 2008). The test used 999 permutations to deliver a pseudo-F statistic and a measure of significance of the homogeneity between clusters (Anderson 2006; Anderson *et al*. 2006; Ricotto and Burrascano 2008). Permutations compare the average distance of lawns in a cluster to the median centre of the cluster (the point in ordination space that minimizes distances between lawns of a cluster) and avoid the need for the assumption of normality (Anderson 2006).

We then used the distance measures to construct a dendrogram of the lawns using furthest neighbour joining in an agglomerative hierarchical cluster analysis. The method initially creates two discrete clusters using lawns that show complete dissimilarity from each other ($\beta = 1.00$). It then adds individual lawns iteratively into these initial groups if their percent covers are similar to the median cover of the lawns already included in the cluster (Price 1999). Further clustering then occurs within these initial groups based on dissimilarity measures to construct the final dendrogram. A cophenetic coefficient was delivered as a measure of goodness of fit of the distances displayed as branch length on the dendrogram to the original dissimilarities between lawns on which the dendrogram is based. Using PERMANOVA analysis, β diversity in grass community structure was compared between each lawn category, as well as between the component lawns of each category in a pairwise analysis.

Average grass percent cover across all species was determined for each category based on total percent covers on the component lawns of each category. The average percent cover of each species within each category was also determined and used to calculate the percent contribution of each species to the total grass percent cover observed in each category.

Soil and grass nutrient status

We used the five soil samples on each lawn to determine the average pH, conductivity and nutrient content for soil on each lawn. The single data point for grass nutrient status was used for each lawn. We then used Mann-Whitney U tests to compare the physical characteristics and nutrient content of the soil, and the nutrient status of the grass between biotic and sodic lawns.

Herbivore presence and utilization

Mann-Whitney U tests were performed on bite mark and dung count data to identify whether there was a difference in 1) mean metabolic biomass of each species 2) mean total metabolic biomass and 3) mean herbivore utilization between lawn types. Using camera trap data, a Kruskall-Wallace test was performed to identify whether total metabolic biomass/hour on the different lawn types differed between seasons. Mann-Whitney U tests were then performed to identify whether total metabolic biomass/hour differs between the late wet season and early-mid dry season on biotic and sodic lawns, respectively.

Using camera trap data, we identified dominant herbivore species across the set of lawns for each season according to their percent contribution to overall metabolic biomass/hour on each lawn. Mann-Whitney U tests were then performed to identify whether each species showed differences in metabolic biomass/hour between biotic and sodic lawns. Metabolic biomass/hour of herbivores in the late wet season was log-transformed for visual clarity. We also determined the proportional contribution of each dominant species to the total biomass or metabolic biomass/hour on each lawn during both seasons.

Dung beetle community assemblage

We obtained a total abundance of each species of dung beetle for each lawn by pooling the abundances from the three traps from both days of sampling. We calculated Bray-Curtis dissimilarities as a measure of β diversity between each lawn based on total species abundances. PERMANOVA analysis was used to identify whether β diversity was different between the *a priori* biotic and sodic lawns identified in this study.

The distance measures were used to cluster the lawns into groups of similarity in a dendrogram, using the same methods for the grass community assemblages above. PERMANOVA analysis was then used to determine whether the difference in β diversity in dung beetle abundance between each hypothesized cluster of lawns was significant. Average species abundance across all morphospecies was determined for each category. The average abundance of each species within each category was also determined and used to calculate the percent contribution of each morphospecies to the total species abundance of each category. This was performed to identify the dominant dung beetle morphospecies and their abundances within each lawn category.

Statistical analyses were performed using R v3.0.1 (2013) and SPSS v 21 (2012) at a significance level of $\alpha = 0.05$. Figures were constructed using R and Excel (2010). All PERMANOVA tests were performed with 999 permutations. Normality was tested for all dependent variables using One-Sample Smirnov-Kilmogorov tests. All displayed means have been reported ± standard error (se).

Results

Grass community assemblages

β diversity across lawns: *a priori* lawn types

A total of 23 grass species were identified across the lawns, nine of which were found exclusively on biotic lawns and six on the sodic lawns (Appendix 2). Of these grass species, 14 were bunch grasses and 9 were mat-forming. β diversity in terms of grass percent cover was higher among the biotic lawns (β = 0.511) than the sodic lawns (β = 0.317) (df = 1, p =0.001). This suggests that lawns displaying highly variable grass species percent cover have been grouped together as biotic, while the lawns identified as sodic are more similar in this trait.

β diversity across lawns: types defined by grass percent cover

Creating lawn categories using a dendrogram

The dendrogram classification of the lawns is a fair representation of the β diversity (pairwise dissimilarity measures) of grass percent cover between lawns (cophenentic correlation = 0.888) (Figure 1). The complete dissimilarity (β = 1.00) approach for dendrogram construction separates the ten lawns into two main subtrees, A and B (Figure 1). A contains all biotic lawns and a single sodic lawn (S5), while B contains all remaining sodic lawns. At β ≈ 0.65, four discrete categories, two within A (I and II) and two within B (III and IV), are observed.

Category I consists of two biotic lawns (B3 and B5) and is referred to as the "biotic type" lawn group. Group II comprises three biotic lawns (B1, B2 and B4), and one sodic lawn (S5). Clustering of biotic and sodic lawns into a single category suggests that lawns displaying grass species percent cover that is intermediate between biotic and sodic lawns exist across the sampled landscape. Group II therefore represents a "mixed type" category containing lawns existing on a biotic-sodic gradient in terms of grass percent cover. Groups III and IV contain closely clustering sodic lawns (S3 and S4; S1 and S2) (Figure 1). Subtree B therefore represents a broad sodic category that includes two sodic subclasses: "sodic type *a*" (III) and "sodic type *b*" (IV).

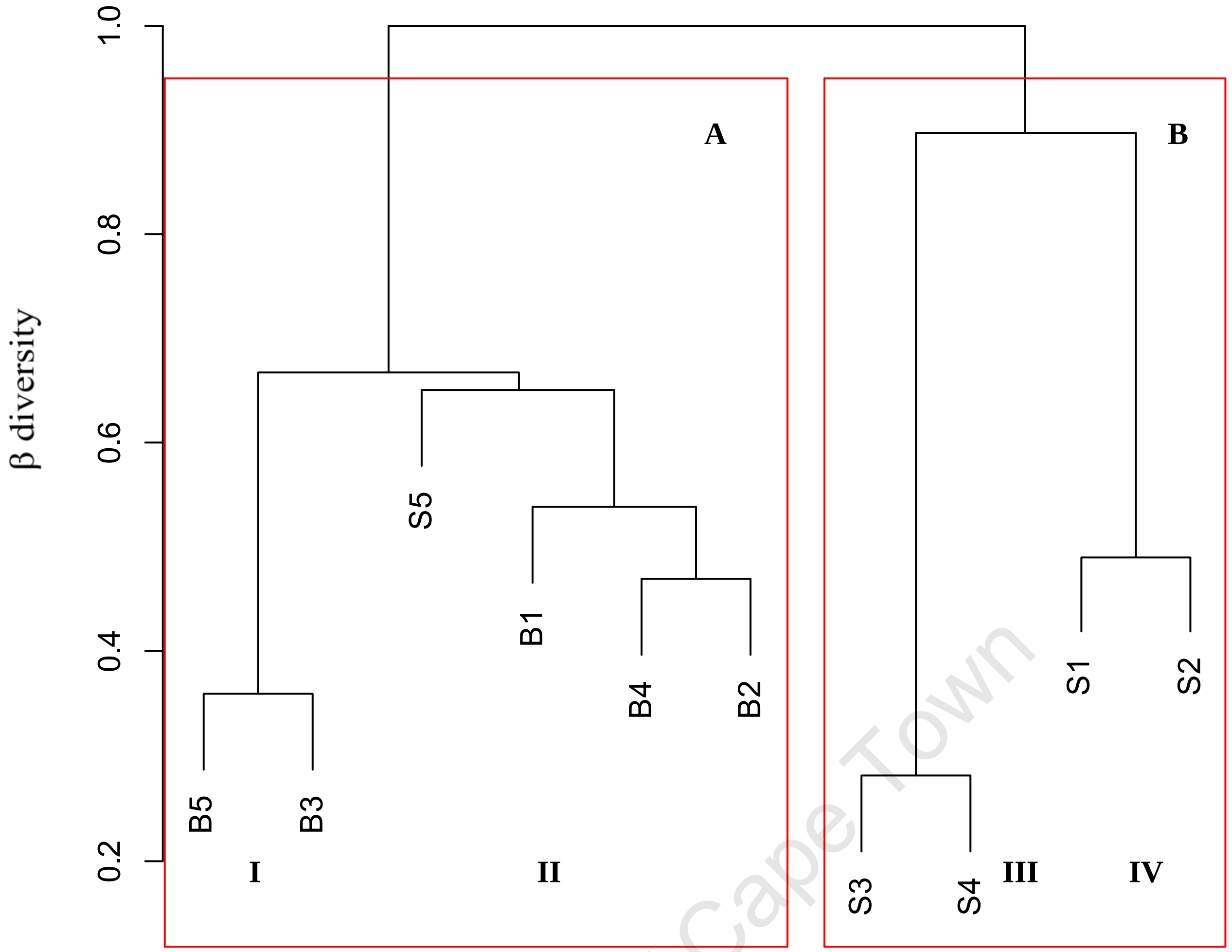

Figure 1. Furthest neighbour joining dendrogram of five biotic (B1 – B5) and five sodic lawns (S1 – S5) based on β diversity in grass percent cover. Two discrete subtrees, A and B, result from the clustering approach that initiates clustering with complete dissimilarity (β = 1.00). At β ≈ 0.65, four clusters representing four discrete lawn-type categories are observed: I = biotic type II = mixed type, III = sodic type *a*, IV = sodic type *b*.

Homogeneity of variance between categories

The average β diversity in grass species percent cover between component lawns of each category (the average distance to the median dissimilarity with each cluster) is significantly different across the four lawn categories (df = 3, p = 0.001). Variance in grass percent cover is significant between all lawn categories that do not fall within the same subtree (A or B) (Table 1).

The longer branching distance between sodic type *a* and *b* suggests that the variance in grass percent cover (β ≈ 0.9) among the lawns within these categories is more different than that observed between the biotic and mixed type categories (β ≈ 0.65). Instead of sodic type *a* and *b* showing similar β diversity, as would be expected from their co-occurence on subtree B, sodic type *b* and the mixed type category display greater similarity (df = 1, p = 0.150) (Table 1).

Therefore, grass percent cover suggests that a lawn identified as sodic may be more characteristically biotic. This is also indicated by the presence of lawn S5 within the mixed type category that is dominated by biotic lawns. The biotic type lawns are distinct from the lawns within subtree B containing only sodic lawns but lack significant difference in grass percent cover variation from lawns of the mixed type category (p = 0.051) (Table 1). Sodic type III is significantly different from all the other categories (Table 1), suggesting that lawns within this group show β diversity in grass percent cover that distinguishes them from the mixed-biotic type lawns..

Table 1. Average β diversity (average distance of each lawn to the median dissimilarity value of their respective categories) among the lawns within the four lawn categories (I – IV). Total grass % cover (± se) is the total grass cover by all species for each category, taken as the average of the total covers of the component lawns of each category. Significance values of pairwise PERMANOVA analysis for homogeneity in grass percent cover between the four lawn categories are also presented. An asterix indicates significant difference in variation (β diversity) in grass percent cover between categories.

Category	**Average β diversity**	**Total grass % cover (± se)**	**I**	**II**	**III**
I	0.180	50.55 ± 9.80	-	-	-
II	0.360	28.34 ± 3.86	0.051	-	-
III	0.140	12.65 ± 2.45	0.004*	0.021*	-
IV	0.256	23.14 ± 4.21	0.002*	0.150	0.001*

Characterizing categories using grass species % cover

The average grass percent cover of each category gives an indication of the percent area of a randomly sampled plot required to be covered by grass (all species) in order to be assigned to each category. A total grass percent cover of 50.55 ± 9.80 % is required to identify a lawn within the biotic type category (Table 1). The lawns of sodic type *a* display an average cover across all species that is distinct (12.65 ± 2.45 %) from the lawns of the mixed type and sodic type *b* categories. The range of percent grass covers observed between the mixed type and sodic type *b* places these two categories on the “intermediate” range between the biotic type and sodic type *b* categories, showing a range in grass cover from 18.93 to 39.35 % (Table 1).

Grass percent covers are more informative about which category a lawn will be assigned to when it is species specific. Total percent grass cover among lawns of the biotic, mixed type and sodic type *b* is made up by both mat-forming and bunched species. However, sodic type *a* only has mat-forming grass species contributing to the total percent cover (Table 2).

Mat-forming grasses contribute the most to the total grass cover on biotic type lawns (66.77%), especially *Digiteria eriantha* (Table 2). *Setaria sphacelata* is the dominant bunch species on these lawns but contributes considerably less to the total percent cover than the mat-forming grass species (Table 2). The intermediate lawns of the mixed type and sodic type *b* are also dominated by mat-forming grasses but the dominant species differs between these categories. *Digiteria eriantha* (38.29%) dominates the lawns within the mixed type lawns while *Dactyloctenium australe* (45.48%) dominates on sodic type *b* lawns. In addition, lawns of the mixed type category show a larger proportional cover by bunch species (38.99%), especially *Eragrostis chloromelas*, than do lawns of sodic type *b* which has only one dominant bunch grass species (*Enteropogon* spp.) (Table 2).

Lawns of the sodic type *a* only had 5 grass species identified between the component lawns (S3 and S4) (*Digiteria eriantha* and *Oropetium capense* showing only 0.4% and 4.34% contribution to total grass cover). *Sporobolus ioclados* was dominant among the lawns with the largest contribution to total lawn percent cover (66.40%) than any other species among the other lawns in the other categories (Table 2).

Table 2. Average percent cover of most dominant grasses (>5 % contribution to total % cover) among the lawns of each category. Total grass percent cover is the average cover across all species within each category, derived form the total grass percent cover on each component lawn.

Lawn category	**Growth form**	**Species**	**Average % cover**	**% contribution to total % cover**
I	**Mat-forming**	*Digiteria eriantha*	21.35	42.24
		Sporobolus ioclados	8.68	17.16
		Eragrostis superba	3.25	7.37
	Bunched	*Setaria sphacelata*	6.4	12.66
		Bothriochloa spp.	4.6	9.10
		Eragrostis chloromelas	3.73	7.37
II	**Mat-forming**	*Digiteria eriantha*	10.85	38.29
		Urochloa mosambicensis	1.74	6.13
	Bunched	*Eragrostis chloromelas*	3.73	13.15
		Bothriochloa spp.	2.71	9.57
		Themeda triandra	2.48	8.73
		Setaria sphacelata	2.14	7.54
III	**Mat-forming**	*Sporobolus ioclados*	8.4	66.40
		Dactyloctenium australe	2.25	17.79
		Eragrostis superba	1.4	11.07
	Bunched	-	-	-
IV	**Mat-forming**	*Dactyloctenium australe*	10.53	45.48
		Sporobolus ioclados	6.93	29.93
		Urochloa mosambicensis	1.54	6.66
	Bunched	*Enteropogon* spp.	2.38	10.26

Decomposer community structure

β diversity across lawns: *a priori* lawn types

A total of 6 228 individuals and 21 morphospecies were collected across the ten lawns over the two days of sampling. All morphospecies were sampled on biotic lawns, while only 18 morphospecies, excluding *Hyalonthophagus* spp., *Garreta* spp. and *Heliocopris* spp. were sampled on sodic lawns

(Appendix 1). β diversity of dung beetle species abundance was higher among the sodic lawns (β = 0.384) than among the biotic lawns (β = 0.178) but this difference was not significant (df = 1, p = 0.068). Therefore biotic lawns will display similar β diversity in dung beetle species abundance as the sodic lawns, even though the sodic lawns are more variable in this trait and form two discrete subgroups.

β diversity across lawns: dung beetle species abundance

Creating lawn categories using a dendrogram

The dendrogram classification of the lawns is a good representation of the β diversity calculated between lawns based on dung beetle abundance (cophenentic correlation = 0.925) (Figure 6). The lawn classification diverges into two discrete subtrees, A and B, at β = 1.00. Subtree A forms one group (I) consisting of two sodic lawns (S2 and S4). Two groups diverge within B at β ≈ 0.7, forming one group containing only biotic lawns (II) and another group containing only sodic lawns (III) (Figure 1). Group II is referred to as the "biotic type" group because it includes all sampled biotic lawns. Groups I and III form sodic lawn categories, referred to as "sodic type a" and "sodic type b", respectively, with III showing greater similarity to the biotic lawn category with which it clusters (Figure 6).

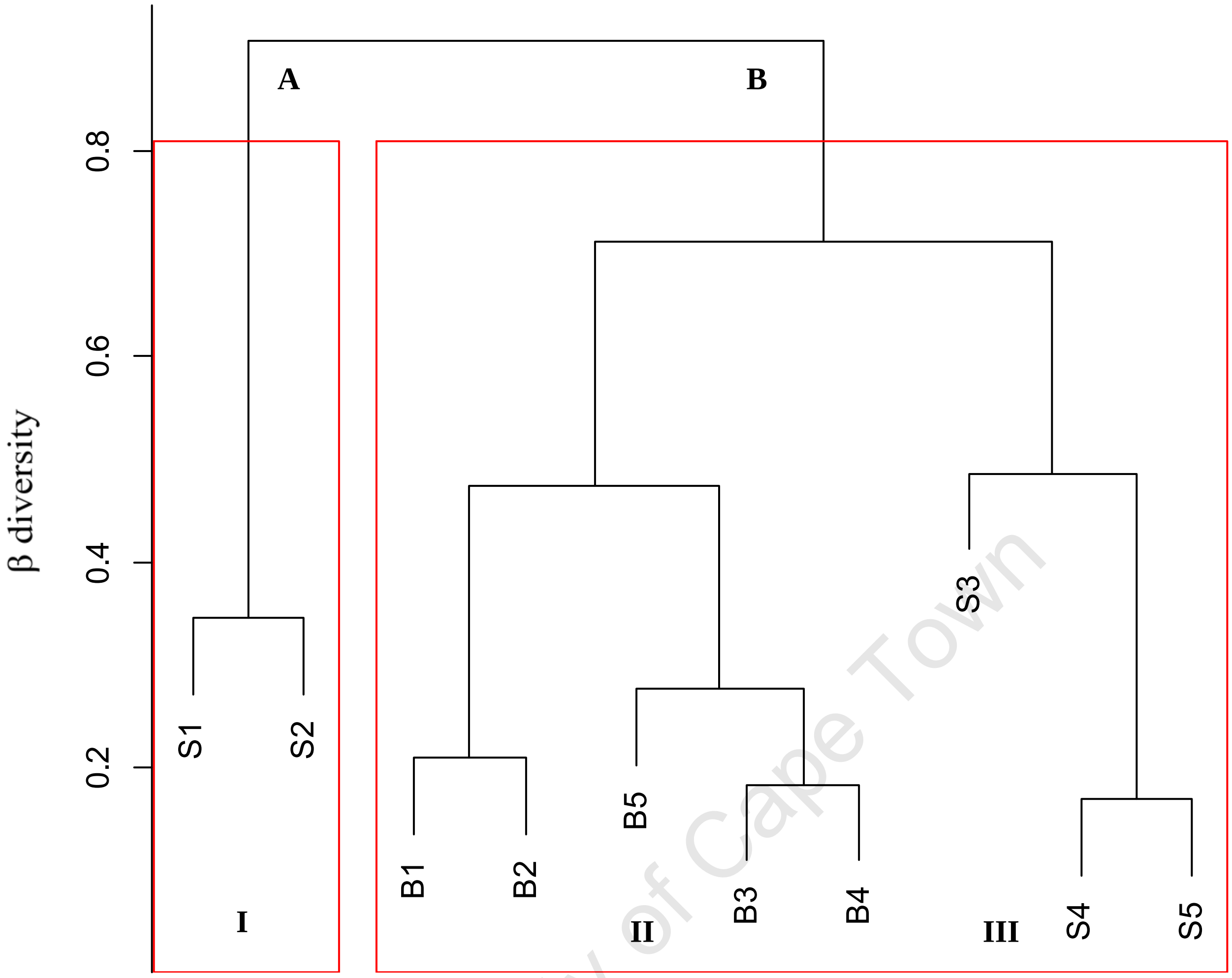

Figure 1. Dendrogram based on β diversity in dung beetle species abundance across five biotic (B1-B5) and 5 sodic (S1-S5) lawns using furthest neighbour joining. Two discrete subtrees A and B result from the clustering approach that initiates clustering with complete dissimilarity ($\beta = 1.00$). At $\beta \approx 0.7$, three clusters representing three discrete lawn-type categories are observed: I = "sodic type a", II = "true biotic", III = "sodic type b".

Homogeneity of variance and characterization of categories

The average β diversity among the lawns within each of the three categories is not significantly different and lawns will display similar species-specific dung beetle abundance to the lawns that it clusters with (df = 2, p = 0.972). This suggests that there is unlikely to be a gradual gradient in the dung beetle species abundances between the three categories but sodic lawns will be divided into two categories showing distinct species abundances (Table 3). Biotic lawns do not cluster with sodic lawns, and vice versa, in any of the categories, again confirming that there is no gradient in species abundance among the lawns between sodic and biotic types. However, the two separate sodic clusters suggest that the identified sodic lawns in this study may be classified into two separate groups that display distinctly different dung beetle species abundances. Therefore, this variation will set the sodic lawns up along a gradient of species abundance, while the biotic lawns are distinct.

In addition, average beetle abundances across all species are also distinct for each lawn category. Total dung beetle abundance across all species decreases distinctly from the true biotic category (371.6 ± 35.70) to the sodic type *b* category (181.67 ± 60.20) and finally to the sodic type *a* category (29 ± 6.00). The unidentified morphospecies consisting of beetles with a body size > 5 mm displays proportional abundances of the total beetle abundance that are distinct for all three lawn categories (Table 3).

Table. Average abundance (± se) of the dominant dung beetle morphospecies/genera (>10% of total abundance) and their percent contribution to the total dung beetle abundance observed within each lawn category. Morphospecies < 5mm includes small-bodied, unidentifiable dung beetles.

Category	Morphospecies/genera	Average abundance	% contribution to total abundance
I	< 5 mm	128 ± 24.54	34.50
	Neosisyphus	134 ± 26.36	36.01
	Onthophagus	48 ± 11.26	12.86
II	< 5mm	19 ± 4.00	65.52
	Kheper	6 ± 1.50	18.97
III	< 5 mm	162 ± 53.92	88.99

Soil nutrient status

A total of 50 soil samples were collected from the ten lawns. Sodic lawns are more basic (pH ≈ 8.0) than the more neutral biotic lawns (pH ≈ 7.0) (U = 1.00, df = 1, p = 0.016) (Figure 2a). Associated with these acidity levels is conductivity which is also higher and more variable on the sodic lawns (621.17 ± 141.46 µS/cm) than on the biotic lawns (204.78 ± 31.89 µS/cm) (U = 1.00, df = 1, p = 0.016) (Figure 2b).

Phosphorous content is variable among both biotic and sodic lawns and shows no significant difference between the lawn types (U = 7.00, df = 1, p = 0.251) (Figure 2c). Potassium content is variable among the biotic lawns but is more constant among the sodic lawns (Figure 2c). On average, biotic lawns display approximately double the amount of K (244 ± 36.71 mg/kg) than sodic lawns (105.32 ± 8.80 mg/kg; U = 0.00, df = 1, p = 0.009). Magnesium content is also distinct between the lawn types, occurring at approximately five times the amount on biotic lawns (10.28 ± 2.66 cmol/kg) than on sodic lawns (2.01 ± 0.437 cmol/kg) (U = 0.00, df = 1, p = 0.009) (Figure 2d). Sodium levels are particularly distinct between the two lawn types and mirror the pattern between lawn types observed for pH and conductivity. Na content is 14 times lower on the biotic lawns (36.84 ± 0.928 mg/kg) than on the sodic lawns (518.68 ± 213.66 mg/kg) (U = 0.00, df = 1, p = 0.009). Variability in Na content is also higher on the sodic lawns than the biotic lawns (Figure 2f).

The first sodic lawn (S1) displays particularly distinct patterns in soil nutrient characteristics. This lawn has the highest and most distinct pH (8.27 ± 0.234), conductivity (1054.56 ± 390.21 uS/cm) and Na content (1328.2 ± 29.96 mg/kg) among all other sodic lawns (Figure 2). In addition, K, Mg and P contents of this lawn are also higher, though less distinctly for K, than the other sodic lawns. Sodic lawns 4 and 5 are also somewhat distinct with similar, though less extreme and, in some cases, variable soil characteristics to S1.

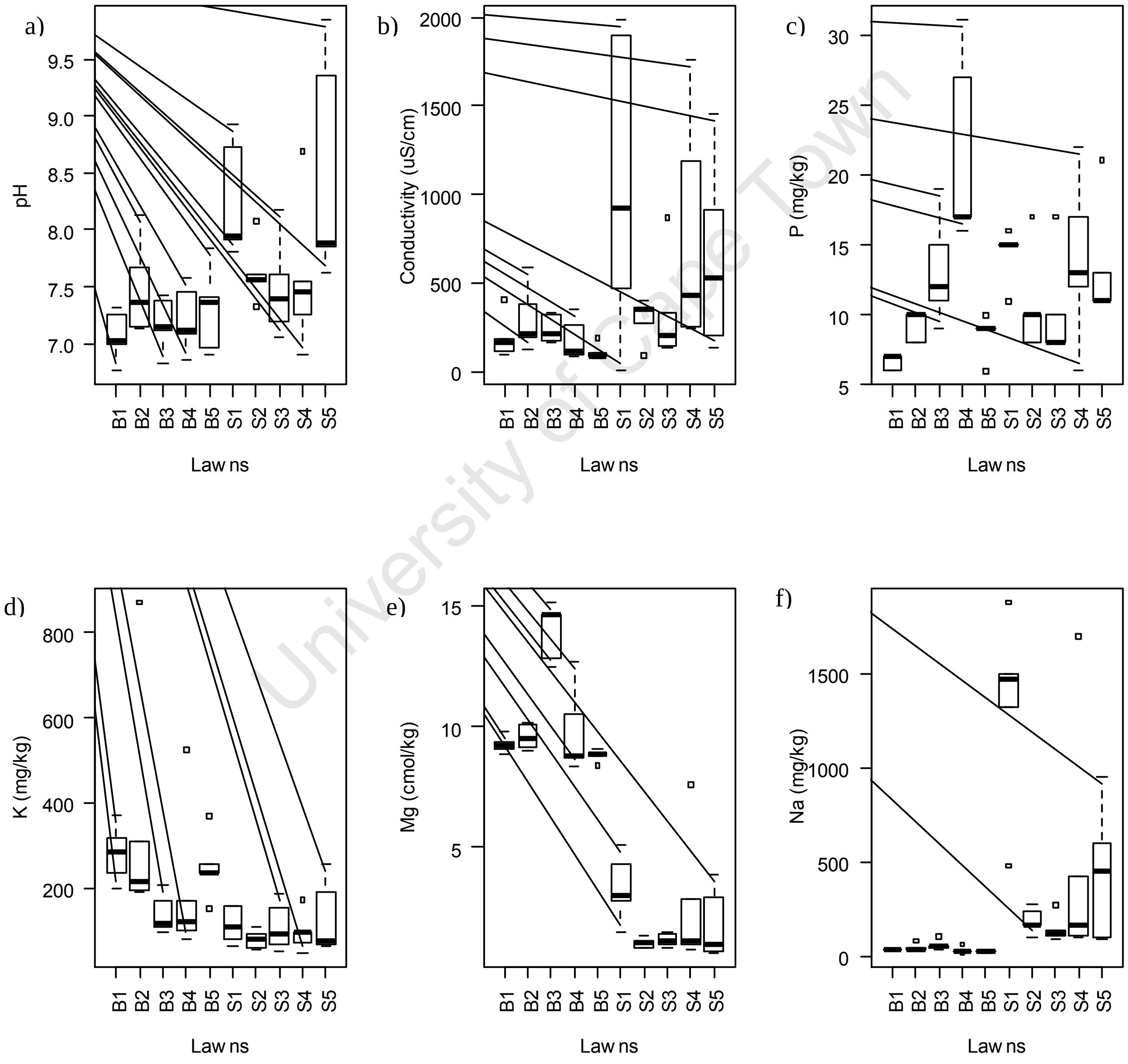

Figure 2. Figures of physical and nutrient status characteristics of soil sampled on five biotic (B1-B5) and five sodic (S1-S5) lawns: a) soil pH b) conductivity (μS/cm) c) P (mg/kg) d) K (mg/kg) e) Mg (cmol/kg) f)

Na (mg/kg). Boxplots represent mean ± standard deviation and ranges in characteristics from the five soil samples taken at each lawn.

Grass nutrient content

A total of ten grass samples, from four different grass species were collected on the lawns. Since foliage was not sampled from the same species on the biotic lawns, the effect of species on grass nutrient status among these lawns should be considered. On average, grass C:N is higher among the biotic lawns (39.31 ± 3.03) than the sodic lawns (24.72 ± 0.91) (U = 0.00, df = 1, p = 0.009) (Figure 3a). The opposite pattern is observed for Na content which is approximately five times higher on the sodic lawns (15 300 ± 4042.28 mg/kg) than the biotic lawns (3010 ± 1307.13 mg/kg) (U = 1.00, df = 1, p = 0.016) (Figure 3b). Among the sodic lawns where the same species (*Sporobolus ioclados*) was sampled, variability in the C:N is low, while Na content shows high variability. In general, grass C:N and Na contents show contrasting levels among the lawns. There is generally a low Na content (3010 ± 1307.13 mg/kg) associated with higher C:N ratios (39.31 ± 3.03) on the biotic lawns. However, the opposite pattern is observed on sodic lawns, where higher Na contents (15 300 ± 4042.28 mg/kg) are observed with lower C:N ratios (24.72 ± 0.91). S1 is also a good indicator of this trend, displaying the highest content of Na (29 000 mg/kg) and the lowest C:N ratio (22.12 %) among all lawns (Figure 3). This sodic lawn also displays the highest Mg and Zn content among all other sodic lawns.

On biotic lawns, there were significantly higher average contents of K (U = 2.00, df = 1, p = 0.028) and Mg (U = 0.00, df = 1, p = 0.009) than on the sodic lawns (Figure 3 c, d). For both of these minerals, *Bothriochloa* sp. on B2 and *Themeda triandra* on B5 display similar contents to that of *Sporobolus ioclados* on the sodic lawns. There is high variability among all lawns in grass Fe content (U = 7.00, df = 1, p = 0.249) and Zn content (U = 4.00, df = 1, p = 0.076), suggesting that there is no effect of grass species or site on these mineral contents (Figure 3 e, f).

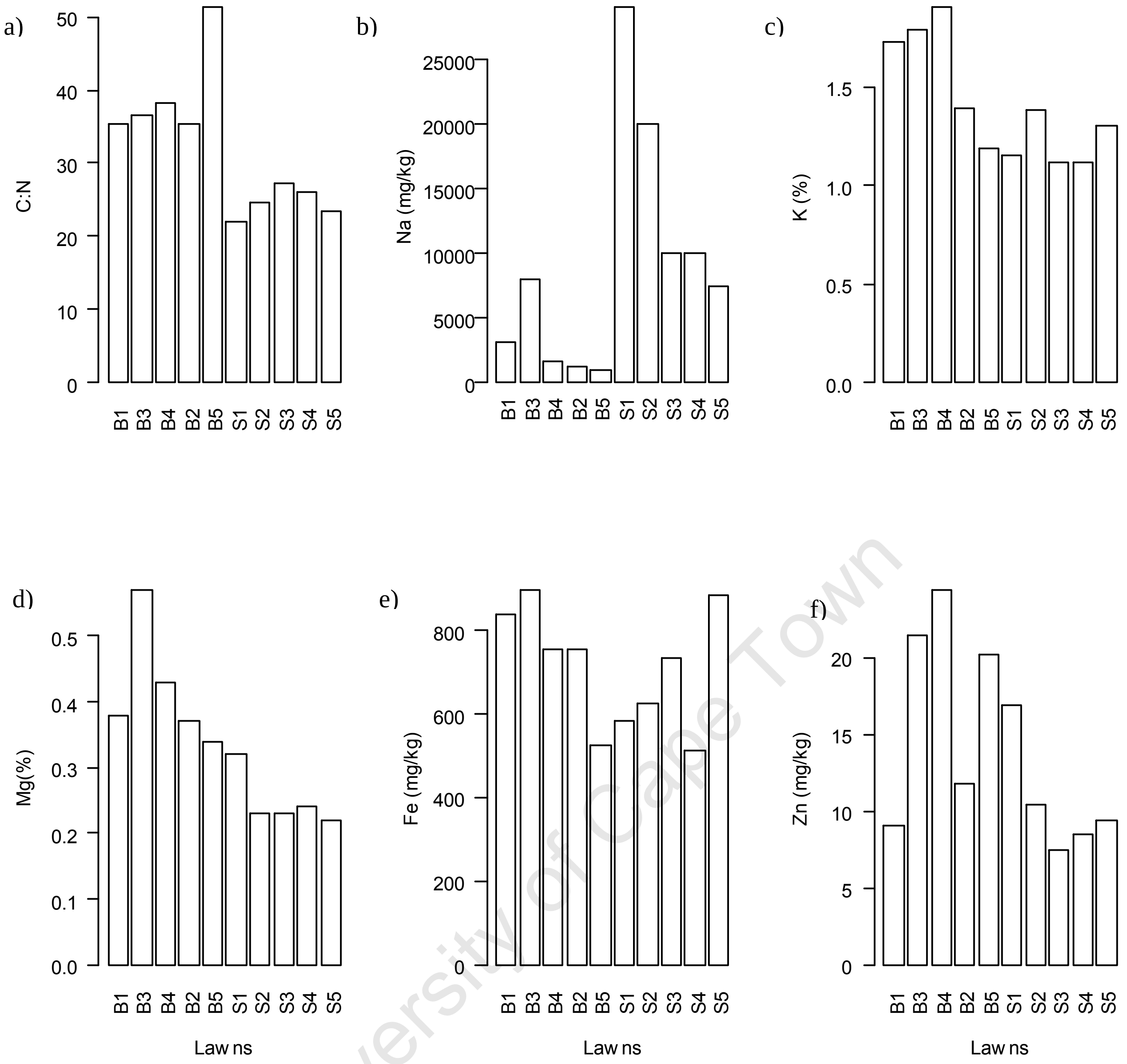

Figure 3. Figures of grass nutrient content on five biotic (B1 – B5) and five sodic lawns (S1 - S5): a) C:N b) Na (mg/kg) c) K (%) d) Mg (%) e) Fe (mg/kg) f) Zn (mg/kg). Lawns with the same sampled dominant grass species (> 50% of total lawn cover) are arranged together for clarity. *Digitaria eriantha* was sampled on B1, B3 and B4, *Bothriochloa* sp. was sampled on B2 and *Themeda traindra* was sampled on B5. *Sporobolus ioclados* was sampled on all sodic lawns.

Herbivore presence and activity

Dung counts and bite marks

Chan *et al*. (2013) identified dung from eight different herbivore species, three of which were grazers (buffalo, rhino and wildebeest), one mixed feeder (impala) and the remaining four species were browsers (elephant, giraffe, kudu and steenbok). On average, biotic and sodic lawns had dung from two species of grazer or mixed feeder present

(1.6 ± 0.245 kg; 2.4 ± 0.245 kg, respectively). Impala was the most commonly observed species dung on both lawns and contributed largely to differences in metabolic biomass across the lawns. Among the sodic lawns, average impala metabolic biomass was higher (143.41± 41.94 kg) than on biotic lawns (95.86 ± 17.05 kg) but this difference was insignificant (U = 10.00, df = 8, p = 0.600) (Figure 4). In fact, impala metabolic biomass contributed 16.5% more to the total metabolic biomass on biotic lawns than on sodic lawns.

Buffalo and wildebeest dung was sampled on both lawns but were both more abundant on the sodic lawns (Figure 4). Buffalo, observed on all sodic lawns, were less abundant but had higher overall metabolic biomass (189.12 ± 84.57) than the gregarious impala and composed 44.8% of the total metabolic biomass on these lawns. Buffalo contribution to total metabolic biomass on biotic lawns (43.4%) was approximately equal to that on the sodic lawns. The difference in buffalo metabolic biomass between lawn types was, therefore, not significant (U = 5.50, df = 8, p = 0.126). Similarly, wildebeest metabolic biomass was higher on sodic (164.86 kg) than biotic lawns (58.29 kg) but contributed equally to the total metabolic biomasses across the two lawn types (6-7%) (Figure 4).

A single rhino dung event was observed on one sodic lawn (S5) but the metabolic biomass of the rhino on this lawn contributed very large proportional metabolic biomass (13.5%) to the total observed over all sodic lawns. On average, the mean total metabolic biomass across all species observed on the sodic lawns (422.48 ± 81.08) was more than double that observed on the biotic lawns (190.09 ± 51.30 kg) but this difference was not significant (U = 4.00, df = 8, p = 0.076) (Figure 4).

Higher mean metabolic biomasses on the sodic lawns (though insignificantly different from that on biotic lawns) result in higher mean herbivore utilization rates (17.25 ± 6.58 %) than on biotic lawns (10.9 ± 2.81 %) (Figure 4). However, this difference is also insignificant between lawns (U = 11.00, df = 8, p = 0.754). The highest herbivore utilization among biotic lawns (21.22 ± 6.17 %) was observed on a lawn with only impala contributing to the metabolic biomass (B1). Surprisingly, wildebeest did not increase herbivore utilization when co-occurring with impala (B5). In addition, lawns where buffalo occurred did not show an increase in herbivore utilization that would be expected due to their higher metabolic biomasses (B3 and B4).

Among sodic lawns, herbivore utilization was surprisingly lowest on the lawn with three species making up a high total metabolic biomass (S1; 4.17%). Similar to the biotic lawns, sodic lawns did not show an increase in herbivore utilization as the metabolic biomass of buffalo or impala increased. Instead, low utilization was observed on the lawn with the maximum buffalo metabolic biomass among the sodic lawns (S3; 6.00%). However, the lawn with rhino contributing to total metabolic biomass showed substantially high, but not maximum, utilization rates (S5; 25.57%) (Figure 4).

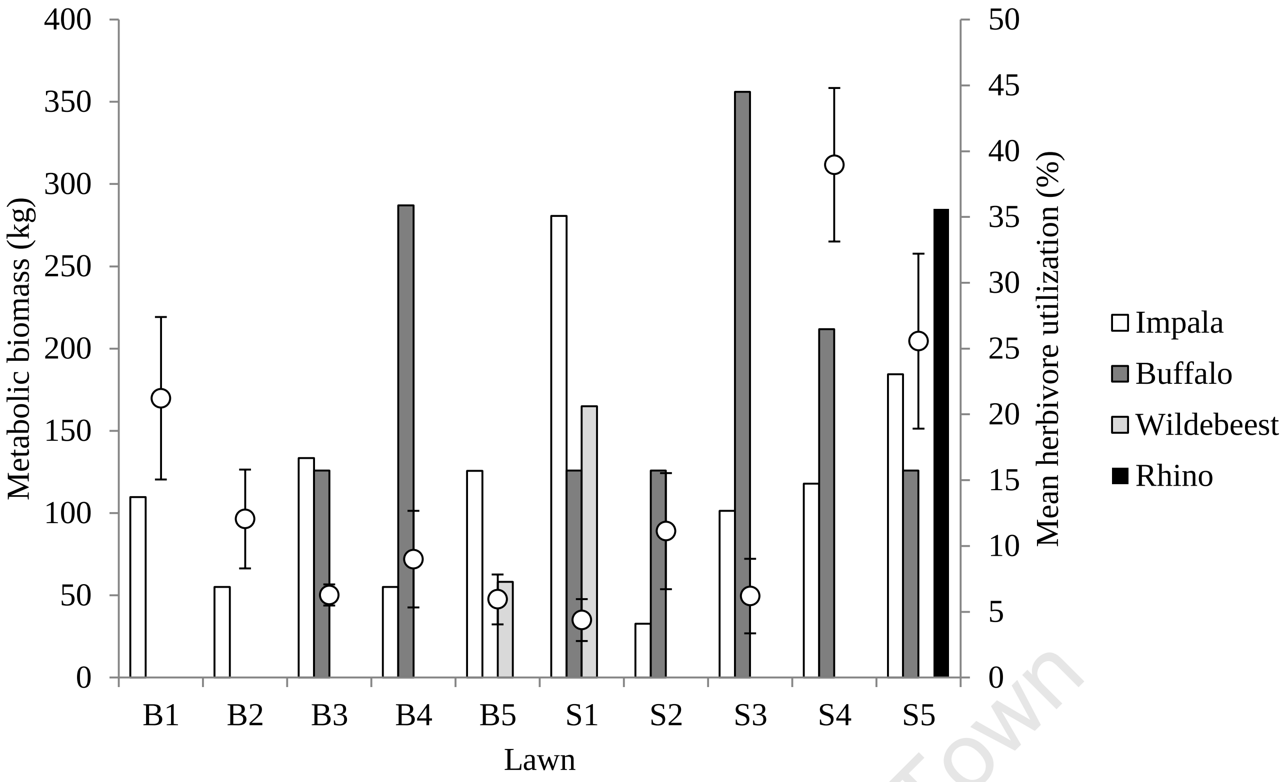

Figure 4. Metabolic biomass from total dung abundance of four identified herbivores and mean (± se) overall herbivore utilization, determined using the percentage of total grass blades that were bitten, across five biotic (B1-B5) and five sodic lawns (S1-S5) in February, 2013.

A total of 104 and 37 independent events were recorded on the lawns, representing an average capture success of 1 independent event in every 10 and 7 hours in February and May, respectively. One trap failed in May, resulting in an average trap success rate of 95%. Between the late wet and early-mid dry season, total metabolic biomass/hour was significantly different between biotic and sodic lawns (Kruskall-Wallis, $F_{2,\ 3} = 8.234$, p = 0.041). The difference in total metabolic biomass/hour on biotic lawns between seasons was significant (U = 1.00, df = 4, p = 0.016). However, total metabolic biomass/hour on sodic lawns was not significantly different between seasons (U = 5.00, df = 4, p = 0.117).

In February, the four dominant herbivores observed on the lawns were impala, rhino, zebra and hippo. Wildebeest were also observed on two biotic lawns (B2 and B4) and warthog were observed on two sodic lawns (S4 and S5) but both of these species showed minimal contribution to the total biomass on their respective lawns (4.1 ± 0.002 % and 4.7 ± 0.03%) (Figure 5a). In May, biomass across the lawns was dominated by impala, buffalo and wildebeest, but hippo, warthog, rhino and zebras were also observed. A single sodic lawn (S5) showed the presence of five of these herbivores, including zebra, while other sodic lawns showed presence of only two species (Figure 5b).

Impala are present on all lawns, except S2, during the late wet season. Mean impala metabolic biomass/hour is approximately equal between the biotic and sodic lawns (3.46 ± 1.34 kg/hr; 3.95 ± 0.67 kg/hr) (U = 10.00, df = 8, p = 0.602) (Figure 5a). However, the presence of impala is more consistent among the biotic lawns than the sodic lawns.

During the early-mid dry season, impala dominate on the biotic lawns but show no difference in their metabolic biomass/hour between lawn types (2.94 ± 1.45 kg/hr; 2.20 ± 1.21 kg/hr) (U = 8.50, df = 8, p = 0.712) (Figure 5b).

Rhino and hippo, both megaherbivores with body masses exceeding 1000kg, show highly variable presence on the lawns between seasons. During the late wet season, hippos were detected only on two sodic lawns and contribute 46.5% and 5.5% to the total biomass on S2 and S5, respectively. On S5, other smaller bodied herbivores, especially impala, contribute more than hippo to the biomass but rhino is the dominant megaherbivore species, contributing 67.4% to the total biomass on this lawn. However, on S2, hippos dominate in the absence of the impala, despite the presence of the rhino. Rhino are present on all lawns, except B2 and S4, where zebra and impala dominate, respectively. Rhino metabolic biomass/hour is generally higher than that of the other herbivores on the biotic lawns but is highly variable on sodic lawns (Figure 5a).

During the early-mid dry season, hippos are only present on a single biotic lawn (B2) and show considerably higher metabolic biomass/hour than the impala, but not the wildebeest which dominate on this lawn. The other biotic lawns are dominated by wildebeest or impala only, all with highly variable metabolic biomass/hours on each. Rhino dominate with the highest metabolic biomass/hour (7.49 kg/hr) on the single sodic lawn (S5), where the biomass of this species makes up 37.8% of the total lawn biomass and 23.6% across all sodic lawns. Buffalo are also observed on the sodic lawns where they were absent in February. They make up a greater proportion (31.2%) of the total biomass and proportion of total metabolic biomass/hour across all sodic lawns (39.4%) than do the larger bodied rhinos (19.3%) (Figure 5b).

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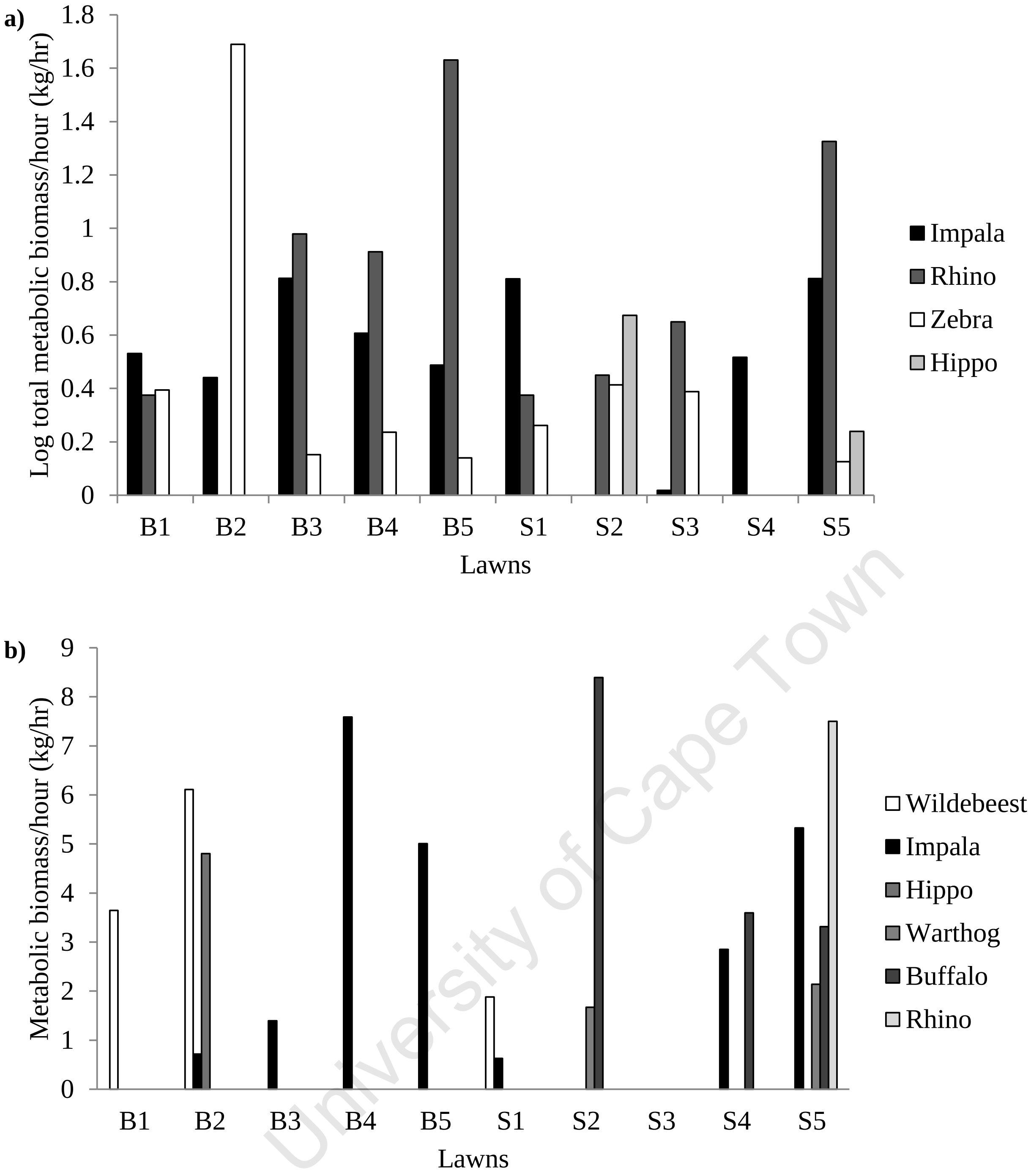

Figure 5. Log-transformed metabolic biomass/hour of four dominant herbivore species during the late wet season (February, 2013) (a) and metabolic biomass/ hour of six dominant herbivore species during the early-mid dry season (May, 2013) (b) across five biotic (B1-B5) and five sodic (S1-S5).

Discussion

Quantitative data on grass, herbivore and decomposer community assemblages and the soil and forage nutrient status was used to investigate differences between biotic and sodic grazing lawns of the Kruger National Park. Sampling of these different aspects of the lawn communities allowed for within and between lawn comparisons on the framework of the positive feedback loop suspected to control maintenance of the lawns. Knowledge of this within- and between-lawn diversity is of significance in the Kruger National Park (KNP), where management schemes aim to preserve and enhance the large scale heterogeneity that is necessary to support the great diversity of flora and fauna in the savanna (Adler *et al*., 2001). Establishing whether grazing lawns contribute large- or fine-scale diversity across the landscape is not only important for maximizing this diversity in landscape and ecosystem, but also for the management of grazing communities that depend on them. The dependence on these highly productive sites by a diverse suite of herbivores, both grazers and mixed feeders alike, will likely become a central idea in future actions to maintain and control these populations.

By identifying differences between biotic and sodic lawns on biotic and abiotic levels of the positive feedback loop, we may establish whether the processes of control and maintenance between the lawn types are identical. This will not only provide insights into the differences in grass, herbivore and decomposer community assemblages and soil properties between the lawns, but also into the relative permanency of the lawn types or vulnerability to ecosystem disturbances. Furthermore, quantifying the relative differences in the biotic and abiotic components will also inform whether sodic and biotic lawns are discrete grazing patch systems in the savanna. The implications of this study for savanna management will differ according to whether the two lawn types only display similarity in being grazing tolerant, short grass patches or are identical across many levels of their maintenance systems. Improved knowledge and understanding of the lawn systems therefore creates avenues for improved and directed efforts in management of their top-down and bottom-up control and maintenance factors throughout KNP.

Grass community assemblages

β diversity levels based on percent cover of 23 different grass species assigned the ten lawns to two separate sets of lawn categories. β diversity within the two discrete sets suggested that the set containing all biotic lawns was highly variable in grass percent cover. This variability was confirmed by the grouping of one sodic lawn with the biotic lawns. This sodic lawn was therefore more characteristically "biotic" relative to the other sampled sodic lawns. Further more, a category containing only sodic lawns displayed identity with this mixed group. Together, these results suggest that a randomly sampled lawn on sodic sites at the catenal footslopes in the savanna may actually be classified as a biotic lawn according to its grass percent cover, due to the variability that the "biotic" category encompasses in this trait.

However, we also identified distinct biotic and sodic categories that displayed characteristic total and species percent cover that would not group them with the other lawn type. Patches where total grass covers approximately 50.5% of the sampled area, with *Digiteria eriantha* and *Sporobolus ioclados* together making up 59% of this cover, will be identified as biotic, while only 13% total grass cover, with *Sporobolus ioclados* making up 66% of this total, is required on a sampled area to identify it as a sodic lawn. These values are obviously scale-dependent and should be applied as indicator values for lawns that are similar in size. Also most notable for lawn identification that a sampled area supporting a zero bunch grass percent cover will be considered sodic. This suggests that the diverse biotic lawns are more susceptible to invasion by bunch grasses, despite the heavy grazing pressure required to maintain them.

Biotic lawns therefore display a greater susceptibility to degradation, in terms of invasion by unpalatable, wiry and sparse species, especially of *Aristida* and *Eragrostis* that are of no value to grazers (Venter *et al*. 2003).

Sodic patches are also commonly perceived as sites of land degradation as well due to their characteristically sparse vegetation or complete land denudation in extreme cases (Khomo & Rogers 2005). Furthermore, exclosure experiments in Kruger National Park have shown that sodic lawns are also susceptible to degradation through invasion by tall-grass species (van Coller *et al*. 2013). The absence of these species on the sampled sodic lawn, however, indicates that grazing pressure is higher than on the biotic lawns to prevent invasion by bunch grasses. To attract this high grazing pressure, grass forage should display greater palatability on these sodic lawns than the biotic lawns. To support this, sodic lawns were confirmed to have grass forage with significantly lower C:N than that on the biotic lawns (but these results were derived from a different set of lawns). This would suggest that the positive feedback mechanism on the sodic lawns is more robust for lawn maintenance than on the biotic lawns.

However, there was no significant difference in the herbivore utilization between lawn types (also based on a separate lawn set). Therefore, high intensity or frequent grazing is required by both biotic and sodic lawns for maintenance. From this perspective, the susceptibility of the biotic lawns to invasion by bunch grass species is counter-acted and the lawn is preserved through grazing activity by herbivores.

As an alternative explanation for the lack of bunch grasses on the sodic lawns, the relative permanency of these lawns across the savanna landscape could be considered. Sodic lawns are considered more permanent features in the landscape (Archibald *et al*. 2005) and this may suggest that sodic lawns are already exposed to longer periods of grazing, without the need for high forage quality to attract grazers. Under this explanation, biotic lawns would therefore require a stronger positive feedback between grazers and grass nutrient status.

In consideration of the above described biotic and sodic categories and the mixed type category containing both identified biotic and sodic, we observe that grass percent cover places lawns along a gradient. The lawns may vary from biotic, through a suite of mixed lawns with both biotic-like and sodic-like traits but are generally more biotic-like, and finally through to sodic. The higher number of lawns categorized as mixed type in this study according to grass percent cover suggest that a randomly sampled lawn in the savanna is more likely to display “mixed-type” lawn traits. These lawns are dominated by either *Digiteria eriantha* (38% of total grass cover) or *Dactyloctenium australe* (46%) but also display high percent covers of *Sporobolus ioclados* (30%) *Eragrostis chloromelas* (13%), *Enteropogon* sp. (10%), *Urochloa mosambicensis* (6-7%) and several other bunch grass species (Table 2).

Decomposer community assemblages

The dung beetle species abundance divided lawns into three distinct groups. Unlike the grass community assemblage, there are no mixed type lawn categories and all randomly sampled lawns will display distinct dung beetle community assemblages. However, while all biotic lawns fall within the same category, sodic lawns form two discrete groups. The biotic lawns are identified by very high total abundances of beetles across all species (ca. 370 beetles after two days of sampling) and will also display high abundances of small (< 5 mm), unidentified dung beetles and medium body-sized beetles of *Neosisyphus* contributing equally to the total abundance (35%). Among the sodic categories, sodic lawns may show either intermediate total beetle abundance (ca. 180 beetles) or very low abundance (ca. 30 beetles). The sodic lawn category with the intermediate abundance will be dominated by the small, unidentified beetles, making up approximately 90% of the beetle abundance. However, the low beetle abundance of the other sodic category is dominated by two morphospecies, namely the small, unidentified beetles (65%) and large-bodied *Kheper* beetles (19%).

The lower abundances of dung beetles observed in both sodic categories relative to that in the biotic category is possibly due to the aridity of the soils that results from severe reductions in hydraulic conductivity associated with extreme accumulation of salts (Khomo & Rogers 2005). This is supported by the Na levels on the sodic lawns that were 14 times higher than on the biotic lawns. This characteristic contributes to the formation of the hard upper soil layer observed among the sodic lawns that makes it difficult for dung beetles to burrow and bury dung. The lack of tunneller species on the sodic lawns confirms this idea.

However, *Kheper* dung beetles observed on the low-abundance sodic lawns are dung rollers rather than tunnellers (Davis *et al*. 2008). This suggests that, even though tunneller species are absent and dung is not returned directly to the soil in burrows, dung decomposition still occurs on the sodic lawns by roller species. Tunneller species were found on the biotic lawns due to favourable soil conditions but these contributed very little (< 10%) to the total beetle abundance of the lawns (Appendix 4). Instead, *Neosisyphus*, a dung roller beetle genera, was dominant on the biotic lawns, suggesting that roller species are equally important for dung decomposition on both biotic and sodic lawns.

The substantially higher abundance of dung beetles on the biotic lawns than on the sodic lawns suggests that dung decomposition plays a more prominent role in the positive feedback loop on the biotic lawns. This conclusion is derived from the observation by Davis *et al*. (2008) that dung beetle activity corresponds to higher nutrient turnover rates. It may be suggested that the biotic lawns require nutrient loading from dung decomposition while sodic lawns do not (Cromsigt & Olff 2008). The relatively high abundance of the small, unidentified beetles on the higher-abundance sodic lawn suggests, however, that not all sodic lawn types are independent of dung decomposition for nutrient turnover. Therefore, sodic lawns exist along a gradient of high to low abundances which is distinct from the biotic lawns, forming their own discrete category with high abundances. Therefore, sodic lawns do not appear to rely completely on abiotic means for the nutrient turnover and, therefore, their persistence.

However, Lubeck *et al*. (2013) identified that lawn type affects beetle size class, with larger-bodied beetles observed on the biotic than sodic lawns. This is also observed in our study with medium-sized *Neosisyphus* beetles dominate only on the biotic lawns, while both sodic categories are dominated by small-bodied beetles. Therefore, biotic lawns will experience a higher rate of dung decomposition and greater nutrient turnover than the sodic sites where the small beetles dominate. This is especially true from the perspective that dung counts of larger herbivores, such as buffalo, were more abundant on the sodic lawns. This suggests that biotic lawns do, in fact, rely more on nutrient turnover by the decomposer community than sodic lawns.

Soil and grass nutrient status

The substantially higher Na levels of the sodic lawns result in more basic soils with very high conductivity levels. In general, these characteristics suggest that the sodic soils are generally more nutrient rich than the biotic lawns, even though Mg and K contents are low. Soil salt content of lawns is an important feature that attracts herbivores to the lawns for utilization, even without the salt manifesting in the lawn forage (McNaughton *et al*., 1997). Salt can be obtained by herbivores and other animals directly from the soil by means of mineral licks, so as to meet their required dietary Na levels (McNaughton 1988). Due to this association with herbivores, Na is even considered to be more important than N and P in initiating grazing pressure required for lawn formation. The high Na soil content on the sodic lawns is due to the underlying parent material (granites) of the sodic lawns (Komo & Rogers 2005). This confirms that abiotic processes are important for maintenance of the soil nutrient status, again linking to the above statement that sodic lawns depend less on decomposer communities for nutrient turnover.

High Na in the soil does appear to manifest in the grass on the lawns. On sodic lawns, Na levels in the grass foliage were 30 times higher than in the soil. A similar but more extreme pattern is observed on the biotic lawns where grass had 80 times as much Na than the soil. This pattern has probably arisen to account for the fact that biotic lawns have lower Na soil content and so accumulate salt to attract the grazers to the lawns for salt-rich foliage rather than salt-rich soils. This is not required on sodic lawns where herbivores can meet all Na requirements from mineral licks.

Evidence has also been presented to show that grazing activity itself increases the Na accumulation capacity of the grasses by exposing soils and increasing hydraulic uplift (McNaughton *et al*. 1997). It may be expected therefore that the grazing pressure on the biotic lawns has resulted in these observed Na patterns between soil and grass. This would suggest that, because sodic lawns also experience high grazing pressure, the grasses on sodic lawns have developed mechanisms to prevent salt accumulation in their foliage. In either case, Na appears to be involved in the positive feedback between herbivores and the grass nutrient status on biotic lawns rather than on sodic lawns.

This being said, Na levels among sodic grasses were significantly higher than among the biotic grasses and this is associated with low C:N among the forage as well. This suggests that grass cover on the sodic lawns is more nutritious and palatable to grazers than the biotic grasses which display opposite characteristics. This is of particular importance for attracting grazers since higher nutrient levels are required to make up for the sparse grass cover on sodic lawns (12% total lawn area covered by grass on 2012 sodic lawns) that would otherwise be insufficient to meet grazer energy requirements (Murray & Illius 2000; du Toit 2003) The higher quality forage resource on the sodic lawns did result in higher grazer utilization on sodic lawns than biotic lawns as determined from bite marks (though the difference is not significant). This grazer activity then translates into the grass material remaining phenologically young and palatable, thereby promoting positive feedback with grazers. In this way, Na levels and C:N encourage the positive feedback loop on sodic lawns for persistence as a short-grass patch.

Herbivore utilization and season

Metabolic biomass of impala is higher on biotic lawns, while buffalo and wildebeest metabolic biomass is higher on sodic lawns. Herbivore utilization is higher on the sodic lawns and this is expected because body size is allometrically scaled with intake rate and specific metabolism (du Toit 2003). However, larger grazers or those that form large herds do not necessarily play as great a role in lawn maintenance than smaller herbivores. Lawns attract herbivores not only to acquire nutrients but also because the lawns offer them a better landscape to detect their predators (McNaughton 1984). From this perspective, metabolic biomass from dung counts on the lawns may be exaggerated relative to the bite mark indicator of utilization. Rhinos may deposit dung in middens on the lawns while impala may spend more time defending territory or searching for mates on these optimal breeding sites (Coetsee *et al* 2010b; Stock *et al*. 2010).

Grazers in large migratory herds are affected by seasonal changes in rainfall and will migrate to wet areas during the dry season in search for high quality forage (McNaughton 1985; Owen-Smith 2002). Grazing lawns do not provide year-round forage resource for these grazers and so food resource availability, quality and distribution decreases during the wet season as the grass cover shifts to a brown herbaceous layer (du Toit 2003). In response to this, there will be an observed decrease in total biomasses from the wet to dry season on the lawns. However, often mesograzers will remain on the lawns during the dry season and will then play a role in the maintenance of the lawns during this time. Mixed feeders in particular show constant presence on the lawns throughout the year despite the variability in the forage resource as they are able to shift guilds from grazers to browsers (du Toit 2003). This is observed using camera trap data between seasons where impala persisted on the lawns from the late wet season to the early-mid dry season. Grazer metabolic biomass remained relatively constant on the sodic lawns between seasons, while biotic lawns had higher biomass during the wet season than the dry season. Wildebeest showed a higher presence on the lawns, particularly the biotic lawns, during the dry season, while rhino were limited to sodic lawns during the dry season though their biomass on both sodic and biotic lawns in the dry season was high. These shifts merely confirm that the megaherbivores migrate in search of nutritious forage away from the lawns as early on in the dry season as May.

A new model of control and maintenance of grazing lawns has been presented that identifies that heavy grazing alone is required to maintain the short, grazing-tolerant grass communities. The main dynamic of this model is that grazers exist in a feedback loop with the grass community to ensure that they obtain food that is of high quality. The cycle is completed by the actual grazing process which keeps the grass sward short and in a young stage of growth. This model is borne from the observation that soil N turnover in East Africa and Hluhluwe-iMfolozi is not significantly different between on and off sites (Coetsee *et al*. 2008; Stock *et al*. 2010). In addition, soil mineralization rates remain constant between open and grazer-excluded areas, suggesting that the positive feedback loop is not required between grazers, grass, soil and decomposer communities for a lawn to be maintained. Instead, the model identifies that seasonal changes in rainfall are responsible for variations in soil nutrient, especially N, content. This suggests that nutrient turnover is driven by abiotic factors.

The results of this study indicate that there are differences between biotic and sodic lawns at the different biotic and abiotic levels of the positive feedback loop. Biotic lawns do appear to require decomposers to return nutrients to the soil from the dung deposited by grazers. Sodic lawns do not depend so heavily on decomposers because their abiotic template maintains soil nutrient levels. Biotic lawns show lower herbivore utilization than sodic lawns, and also display distinct grass percent cover of different grass species than the sodic lawns. Soil nutrients manifest in the grass foliar material on biotic lawns, while sodic lawns display grass nutrient levels independent of soil traits, suggesting that soil, grass and herbivores are not inter-linked. We therefore conclude that biotic and sodic lawns represent distinct lawn types in the savanna.

Both are herbivore driven systems in the savanna, relying on frequent and intense grazing to prevent invasion by tall bunch grass species and lawn degradation. What differs between the sodic and biotic lawns is the maintenance of their nutrient levels through different cycle. Biotic lawns are, indeed driven by biotic interactions and sodic are driven by their abiotic template. In consideration of the new model presented above, we may also suggest that the biotic lawns are also driven by abiotic factors, especially rainfall. Finally, grass species percent cover and dung beetle abundance suggest that lawns identified as sodic and biotic actually exist along gradients in community assemblages. The strict dichotomy between sodic and biotic lawns does not always encompass the β diversity observed among the lawns. Essentially, however, all lawns in the savanna landscape will display control and maintenance factors that are sodic (abiotic-driven) or biotic, but their intrinsic characteristics, in terms of community assemblages are not always as distinct.

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