BINDURA UNIVERSITY OF SCIENCE EDUCATION

IMPLICATION OF ABANDONED CATTLE ENCLOSURES ON UNGULATE HERBIVORY, PLANT SPECIES AND MACRO-INVERTEBRATE DIVERSITY IN SAVE VALLEY CONSERVANCY, ZIMBABWE

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APPROVAL FORM

The undersigned certify that they have supervised, read and recommend to the Bindura University of Science Education for acceptance a research project entitled: "**Implication of abandoned cattle enclosures on ungulate herbivory, plant species and macro-invertebrate diversity in Save Valley Conservancy, Zimbabwe"** in fulfilment of the requirements for the degree of **Master Of Philosophy in Ecology**

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ABSTRACT

African savannas are experiencing a shift in land-use, away from livestock farming towards wildlife conservation. The abandoned livestock areas may have implications on biodiversity and ecosystem functioning, as they create valuable nutrient-rich patches across the dystrophic semi-arid savanna. This study aimed at assessing the influence of abandoned kraals on the interactions between herbivory and plant assemblages, taxonomic and functional diversity of macro-invertebrates on a 22 year old abandoned cattle ranching site in Save Valley Conservancy. We tested whether the abandoned kraals were still soil nutrient-rich. We further studied vegetation structure and composition, forage properties, herbivory, taxonomic and functional composition of macro-invertebrates. After 22 years, the abandoned kraals still show significantly higher concentrations of soil nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), sodium (Na) and organic carbon (C). Although, herbaceous (grass and forbs) productivity was higher on abandoned kraals, herbivory was more pronounced on grass forage species with increased foliar nutrients than forb forage species. Only herbaceous biomass for grasses had a significant influence on the interaction between plants and herbivory while no clear relationships were observed between forage quality and herbivory and plant species diversity. Macro-invertebrate richness was generally high on abandoned kraals and only the species diversity of the belowground taxa responded significantly to the influence of abandoned kraals. Soil nutrients and herbaceous productivity had strong positive correlations with the abundant belowground and aboveground taxa respectively. At functional level, abandoned kraals had the higher functional richness, functional divergence and functional dispersion when both aboveground and belowground species are combined. However, much of the functional diversity indices were significantly high for the belowground habitat. This is a novel finding suggesting the vulnerability of the belowground habitat to resource patchiness. Functional response groups did not vary between kraals and controls indicating that the habitat is in the process of recovering to stability. The study concludes that abandoned kraals are nutrient-hotspots with potential of influencing soil-plant-herbivore interactions, taxonomic and functional assemblages of macro-invertebrates.

DECLARATION

I do hereby declare that this thesis was composed by me and has not been accepted in any previous application for a degree. The work of which it is a record was carried out by me and all sources of literature have been acknowledged by means of references.

Signature: ..... **Date: .....**

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DEDICATION

To my beloved daughter, Cedrica –a future conservationist

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CHAPTER 1

INTRODUCTION

1.1 Background to the study

Savannas are heterogeneous ecosystems governed by the interaction of soil nutrients, herbivory, soil moisture and fire (Adler et al., 2001; Scholes & Archer, 1997; van Langevelde et al., 2003). They cover 65% of Africa. The savannas are of great socio-economic importance mainly for human, livestock production and wildlife conservation (Riginos et al., 2012; Solbrig et al., 1996). Therefore, understanding how habitat heterogeneity influence the connections between vegetation, herbivory and biodiversity become a fundamental goal in savanna ecology. Temporal and spatial heterogeneity is driven by climate variability, underlying geology, landscape structure, and land-use practices among other factors (Adler et al., 2001; Du Toit et al., 2003; Huston, 1999; Scheffer et al., 2001). At a local scale, habitat heterogeneity is chiefly determined by the factors that influence quantity and quality of feed resources (Mathieu et al., 2005; Seibold et al., 2016) and nutrient hotspots (Coller & Siebert, 2015; Grant & Scholes, 2006; Holdo & McDowell, 2004; Muchiru et al., 2009). In the past two decades, abandoned kraals have been a subject of research focus as potential nutrient hotspots (Porensky & Veblen, 2015; Riginos et al., 2012; Young et al., 2005). However, it remains debatable whether or not abandoned kraals act as nutrient hotspots across all environments where they are found (Porensky & Veblen, 2015). For instance, some studies on termite mounds contended the general observation that they are nutrient-hotspots across all the environments they occur (Muvengwi et al., 2013; van der Plas et al., 2013). Hence, this calls for more empirical studies before general conclusions are made.

Throughout much of the African savannas, cattle ranching and pastoralism is a common phenomenon. However, due to economic advantages of wildlife conservation over cattle ranching, more cattle ranches have been converted to wildlife production in the recent past (Kioko et al., 2012; Lindsey et al., 2008, 2013; Young et al., 1998). Livestock ranching has become uneconomical due to droughts, pests, diseases and poor markets access while net gains from wildlife-based tourism are increasing (Lindsey et al., 2008; Waterhouse, 1994; Young et al., 1998). This shift in land-use has left persistently nutrient-rich habitat patches embedded in a nutrient-poor savanna landscape (Muchiru et al., 2009; van der Waal et al., 2011; Veblen & Young, 2010). The existence of such nutrient-rich patches contributes to habitat heterogeneity, with profound effects on ecosystem services and functioning. This is important because variation in soil fertility levels in the savannas governs the interaction between plant and animal assemblages with a potential to influence biodiversity (Du Toit et al., 2003).

Substantial work has been covered on the ecology of nutrient-hotspots in African savannas. In particular, termite mounds (Holdo & McDowell, 2004; Mobaek et al., 2005), abandoned cattle enclosures (Porensky & Veblen, 2015; van der Waal et al., 2011), geomorphologic units (Grant & Scholes, 2006), former human settlements (Muchiru et al., 2009; Söderström & Reid, 2010) and artificially fertilised plots (Pretorius et al., 2011). In all cases, nutrient hotspots were found to have disproportionately higher productivity and herbivore use than the surrounding matrix. Abandoned livestock areas (*e.g.* pastures, kraals, corrals and bomas) as a form of anthropogenic nutrient-hotspots with high nutrient concentrations and distinct vegetation, have spawned a great interest in ecology over the past two decades (Riginos et al., 2012; Young et al., 1998). However, most of the studies are fragmented, some focusing on edaphic characteristics (Kizza et al., 2010), habitat productivity (Young et al., 2013), vegetation structure and composition (Manier & Hobbs, 2007; Veblen &

Young, 2010), herbivory and habitat use (Augustine et al., 2003; van der Waal et al., 2011) and selected macro-invertebrate taxa (Warui, 2004; Wilkerson et al., 2013).

Abandoned kraals can bring ecological cascading effects on the affected ecosystems in the form of soil-plant-herbivore feedbacks (Augustine et al., 2003; van der Waal et al., 2011) and edge effects (Porensky et al., 2013; Riginos et al., 2012). On abandoned kraals, limiting soil nutrients (N, P, K, Mg, Na, Ca and organic C) can be four-fold higher than on surrounding matrix (Kizza et al., 2010; Veblen & Young, 2010). In turn, this stimulates high herbaceous productivity of palatable forage which attracts ungulate herbivores (Augustine et al., 2003; Grant & Scholes, 2006; van der Waal et al., 2011). Foraging herbivores further enrich the sites through deposition of dung and urine (Augustine et al., 2003). In the process, nutrient enrichment by foraging herbivores constraints woody species recruitment in favour of grasses (van der Waal et al., 2011) thereby creating open habitat patches preferred by prey species (Riginos et al., 2012). On the other hand, the abrupt transitions of vegetation and soil properties create edge effects which do not only affect habitat use by mega-herbivores (Porensky et al., 2013), but the resource-sensitive macro-invertebrate assemblages (Ayuke et al., 2009; Warui, 2004; Wilkerson et al., 2013). Macro-invertebrate richness and abundance has been demonstrated to proliferate in micro-habitats of improved soil physio-chemical properties (Decaëns et al., 1998; Doblas-Miranda et al., 2008) and vegetation structure and composition (Haddad et al., 2001; Laossi et al., 2008).

However, it is not yet clear how abandoned kraals influence the interactions between herbivory and forage quality, structure, diversity and productivity. More so, there is scarce of information on African savannas and on how macro-invertebrate taxonomic and functional assemblages are being influenced by such anthropogenic disturbances (Warui, 2004). These issues form the basis of this thesis and are addressed using abandoned kraals (22 years after

use) in Save Valley Conservancy (SVC) in southeast Zimbabwe, a semi-arid savanna ecosystem.

1.2 Research problem

The abandoned kraal sites in SVC have been a concern in habitat management as casual observations showed that local distribution of ungulate herbivores is to some extent influenced by these sites. There is an overutilization of abandoned kraal sites through grazing and browsing (Chikorowondo, personal observation). Little is known on how these unnatural habitat patches impact on biodiversity, ecosystem services and functioning since no ecological studies have been carried out since their last use 22 years ago. Ecologically, abandoned kraals are nutrient-rich productive sites (Young et al., 1998) and have the potential to influence plant community development (Muchiru et al., 2009; Veblen, 2012), herbivory patterns (Augustine et al., 2003; Grant & Scholes, 2006; van der Waal et al., 2011) and biodiversity (Porensky et al., 2013; Warui, 2004; Wilkerson et al., 2013). It is not yet clear whether increased herbivory on nutrient-rich sites is as a result of altered vegetation structure and composition (Veblen, 2012), forage nutrition (Augustine et al., 2003; Grant & Scholes, 2006; van der Waal et al., 2011), soil nutrient status (Muchiru et al., 2009; Pretorius et al., 2011) or openness of the habitat (Augustine & McNaughton, 2006; Riginos et al., 2012). Also, there is little information on macro-invertebrate response to abandoned anthropogenic sites in African savannas. As noted by Warui (2004), loss of particular macro-invertebrates and their associated functions can have profound effects on food-webs and ecosystem functioning. Therefore, this study seeks to bridge the gap on how abandoned kraals influence the interaction between herbivory and plant assemblages as well as the taxonomic and functional assemblages of macro-invertebrates.

1.3 Justification

Habitat heterogeneity has been suggested to influence the dynamics in biodiversity and tree-grass production chiefly being determined by soil nutrient availability, herbivory, fire and rainfall (Sankaran et al., 2005; Scholes & Archer, 1997). Of the four major determinants, soil nutrients and herbivory have received less attention in African savannas (see van der Waal, 2010). Similarly, the ecological implications of the growing land-use shifts from livestock farming to wildlife conservation in African semi-arid savannas are still an environmental problem confronting wildlife managers (Lindsey et al., 2013; Riginos et al., 2012). Therefore, improving the understanding of how anthropogenic habitat changes influence biodiversity, plant and animal assemblages is of increasing importance in conservation.

In ecology, anthropogenic-disturbed habitat patches have been invoked to explain the variations and interactions between herbaceous species productivity, herbivory and biodiversity (Du Toit et al., 2003). This can be well-explained by ecological theories. For instance, under the productivity-diversity hypothesis (Grime, 1973; Huston, 1979), species diversity is expected to be high at intermediate levels of productivity as low and high extremes may set in environmental stress and competitive exclusion, respectively. Thus, it is hypothesised that abandoned kraals are sites of high production in terms of soil nutrients and herbaceous biomass and would harbour high macro-invertebrate richness and abundance. Furthermore, macro-invertebrate taxonomic richness is regarded as a good surrogate of functional richness (Díaz & Cabido, 2001), hence we hypothesised that functional diversity would be higher on abandoned kraals. Also, the information gap on the link between plant assemblages and herbivory on abandoned kraals could be explained by the optimal foraging theory (Pyke, 1984) which generally states that herbivores tend to forage in areas where intake rate is high, predation risk is low and the forage is much palatable which gives them a high fitness pay-off (Owen-Smith & Chafota, 2012; Owen-Smith & Cooper, 1987).

A better understanding of the ecology of abandoned kraals is of importance to agro-pastoralists and wildlife managers who should be well informed of far reaching consequences of these small habitat patches on biodiversity and ecosystem functioning (Riginos et al., 2012). Moreover, in their quest to promote a high spatial heterogeneity (Du Toit et al., 2003), ecologists would therefore factor in the consequences of nutrient patchiness in their thinking when managing and studying the semi-arid savannas.

Research focused on abandoned kraals as an example of an anthropogenic nutrient-hotspot have several justifications. First, limited knowledge exist on the ecosystem response to abandoned kraals since their abandonment (22 years ago) in SVC. Second, previous studies on abandoned kraals done elsewhere were fragmented *i.e.* considered separately the confounding effects of soil properties, plant structure and composition and forage nutrition (Augustine et al., 2003; van der Waal et al., 2011; Veblen, 2012). It is still not clear how abandoned kraals influence the combined interactions between plant and animal assemblages. Third, very little is known about macro-invertebrate assemblages in disturbed ecosystems in semi-arid savannas and a few available studies were done on selected common taxa (Ayuke et al., 2009; Warui, 2004; Wilkerson et al., 2013). It has been demonstrated that most guilds of macro-invertebrate are influenced by resource patchiness at a fine scale (Decaëns et al., 1998; Hemerik & Brussaard, 2002) and t play very important roles in ecosystem functioning (Lavelle et al., 2006). Fourth, provision of a natural resource inventory in disturbed ecosystems is very crucial for monitoring long-term biodiversity changes (Dangerfield, 1997; Warui, 2004). Shortage of macro-invertebrate checklists was reported to be the major impediment to macro-invertebrate studies and biodiversity monitoring in African savannas (Warui, 2004). Fifth, there is a growing trend on the assessment of functional assemblages along with taxonomic assemblages in order to fully understand the effects of a disturbance to ecosystem processes and functioning (Cole et al., 2006; Díaz & Cabido, 2001; Petchey & Gaston, 2006). This is important because the

stability or resilience of an ecosystem after a disturbance can be predicted (Joseph et al., 2014; Mumme et al., 2015) Moreover, limited research efforts have attempted to assess the functional response of macro-invertebrates to anthropogenic nutrient hotspots in semi-arid savannas. Therefore, this study aimed at assessing the interactions between animal and plant assemblages, taxonomic and functional assemblages of macro-invertebrates. The focus on SVC as the study site, is chiefly because it is one of the largest conservancies in the world (Lindsey et al., 2008) with remnant abandoned kraals from cattle ranching which presents an excellent opportunity for such a study. Findings of this study will immensely contribute to the management of anthropogenic nutrient hotspots in semi-arid savannas and provide useful insights for future ecological researches in semi-arid savannas.

1.4 Research objectives

The overarching aim of this study was to assess how abandoned kraals (as sources of habitat heterogeneity) influence soil nutrient status, vegetation structure and composition, herbivory and macro-invertebrate assemblage. Given that abandoned kraals are long-term, nutrient-rich habitat patches, high values are expected for vegetation structural and compositional variables as explained by the productivity-diversity hypothesis. Moreover, forage quality as well as grazing intensity is expected to be high as herbivores tend to follow nutritious forage. Abandoned kraals are also considered as micro-habitats (with improved resource quality and quantity) for the establishment of macro-invertebrates.

Therefore, the study was guided by the following specific objectives;

a) To assess whether soil enriched most from cattle dung and urine (during cattle ranching era) is still detectable after 22 years of kraal abandonment.
b) To assess whether abandoned kraals influence vegetation structure, composition, productivity and palatability.

c) To assess the relationship between mammalian herbivory and forage quality, structure and composition.
d) To compare macro-invertebrate diversity between abandoned kraals and surrounding savanna.

This study seeks to bridge the gap in knowledge regarding how abandoned kraals (22 years after abandonment) in SVC influence the interplay between soil nutrients, herbivory and vegetation structure, composition and productivity using sound ecological assessment techniques (Anderson & Ingram, 1993; Grant & Scholes, 2006; Walker, 1976) and multivariate data analyses (Lepš & Smilauer, 2003). Moreover, this study addresses the information gap on the biodiversity response of macro-invertebrates (taxonomic and functional) by employing the recently introduced distance-based multivariate techniques for measuring functional diversity (Laliberte & Legendre, 2010; Mouchet et al., 2010; Petchey et al., 2004).

1.5 Study area

The study was conducted in SVC, south-eastern Lowveld of Zimbabwe (20°05´S, 32°00´E) which covers an area of about 3387 km^2 divided into 23 individual properties with 18 management units (Fig. 1.1). The area lies in the savanna semi-arid zone of Zimbabwe and falls within Agro-ecological Region (v) which has a mean daily temperature of 35°C and variable annual rainfall that ranges from 300-500mm per annum (Lindsey et al., 2008). Gneisses and paragneisses rocks form the larger part of the geology with gently, undulating terrain and scattered kopjes. The south-eastern part of SVC has a great geological diversity, with the surface rocks including Umkondo limestone, quartzites, sandstones and extensive dolerite intrusions (Lindsey et al., 2008). Vegetation is mainly deciduous open woodland savanna dominated by *Colophospermum mopane*, *Combretum* sp., and riverine thickets (Waterhouse, 1994). Herbaceous community is dominated by a mixture of annual and perennial grasses such

as *Setaria*, *Panicum* and *Cenchrus* species). Historically, this area was predominantly used for cattle ranching until 1991 when a land-use audit reported that game farming was more profitable than cattle ranching (Waterhouse, 1994) The former Devuli cattle ranch, was then divided into smaller land units that shifted from cattle ranching to wildlife conservation. In 1992, wildlife was successfully re-introduced in large numbers from other local conservation areas and today the SVC stands testament to one of the grandest African conservation visions of all time (Lindsey et al., 2008). Among its diverse wildlife species, there is the big five: elephant (*Loxodonta africana*), buffalo (*Syncerus caffer*), leopard (*Panthera pardus*), lion (*Panthera leo*), black rhinocerous (*Diceros bicornis*), white rhinocerous (*Ceratotherium simum*) and other ungulate herbivores, including zebra (*Equus quagga*), giraffe (*Giraffa camelopardalis*), impala (*Aepyceros melampus*), sable antelope (*Hippotragus niger*) and hippopotamus (*Hippopotamus amphibius*).

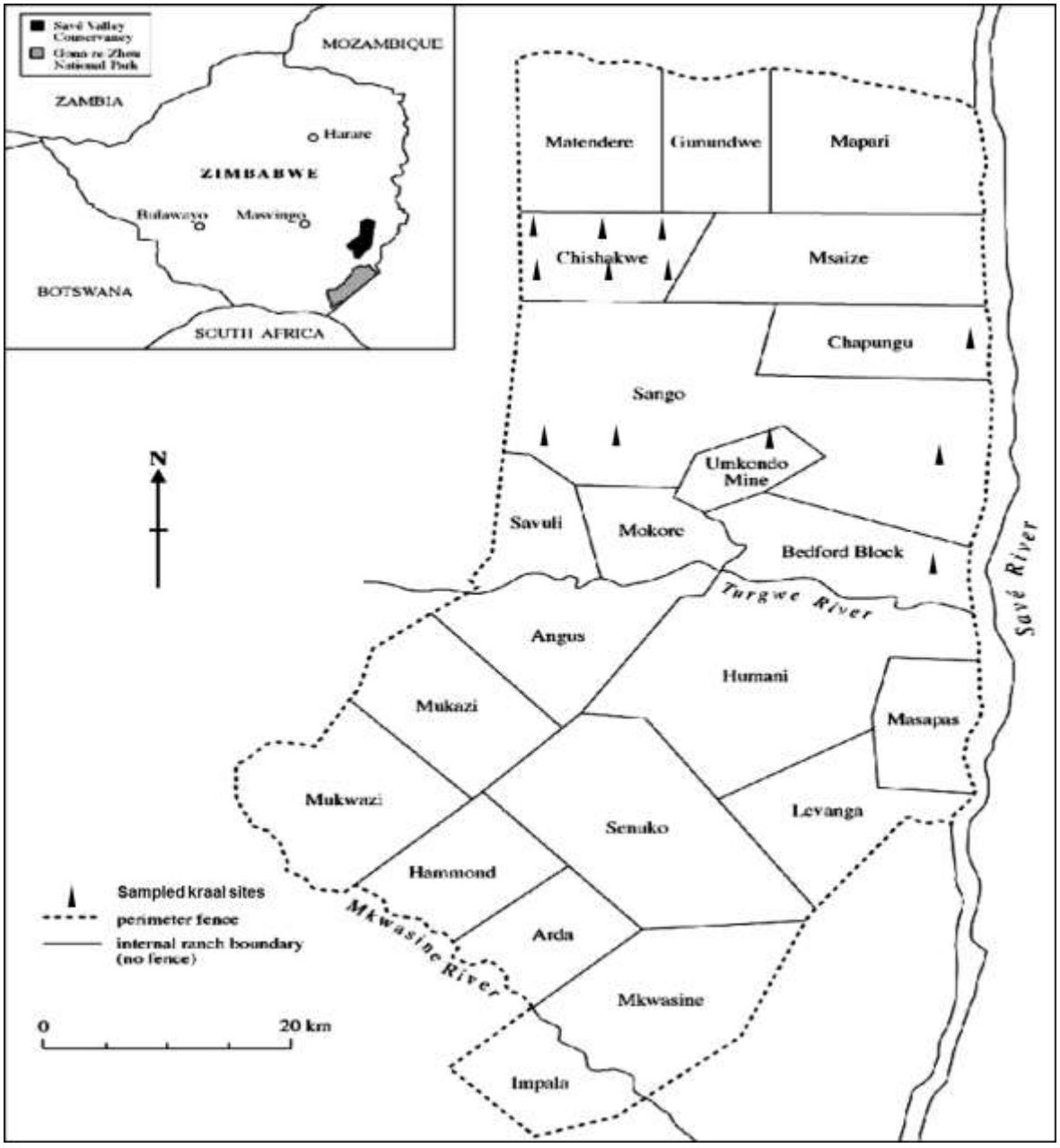

Figure 1. Map of Zimbabwe, Save Valley Conservancy (after Lindsey et al. 2008) indicating SVC and the sampling sites.

1.6 Layout of the thesis

The thesis consists of six chapters contributing to the understanding of the ecological implications of abandoned kraals in a semi-arid African savanna ecosystem. These include Chapter 1 (this introduction), Chapter 2 (Literature review) and three data chapters (Chapters 3-5) presenting the original research and the general discussions, conclusions and recommendations (Chapter 6).

DISCLAIMER: Some sections of the thesis will be repeated in published data chapters 3-5 as they are presented as full original articles.

Chapter 2, reviews the ecological implications of nutrient hotspots in African savannas and includes a review of previous studies situating the research gap which this study seeks to cover.

Chapter 3, examines the interaction between herbivory, plant productivity, quality, diversity and structure at twelve abandoned kraals (22 years later) contrasted with their paired controls in SVC. The main aim of this chapter was to better understand the leading factors behind the linkage between herbivores and plant assemblages influenced by abandoned kraals. Although ungulate herbivores are often attracted to high quality and quantity of forage resources (Augustine & McNaughton, 1998; Du Toit et al., 2003; Grant & Scholes, 2006) usually growing on predator-free habitat patches (van der Waal et al., 2011; Veblen, 2012), little is known regarding their interaction with vegetation variables on abandoned kraals in semi-arid savannas.

Chapter 4, analyses the influence of habitat productivity (soil and plant) on macro-invertebrate assemblage composition. Abandoned kraals as high productive habitat patches (Muchiru et al., 2009), were contrasted with control plots from the surrounding savanna landscape for above and belowground macro-invertebrates. Macro-invertebrate richness is known to be positively correlated to soil nutrients (Doblas-Miranda, Sánchez-Piñero, et al., 2009) and plant structure and composition (Haddad et al., 2001).

Chapter 5, analyses the influence of abandoned kraals on functional diversity of macro-invertebrates. To our knowledge, this is the first study to assess the influence of abandoned kraals on functional diversity of macro-invertebrates in southern African savannas. The study

aimed to assess whether abandoned kraals are influencing the ecosystem functioning by hosting a high abundance and richness of macro-invertebrates. Using distance-based multivariate approaches, we classified macro-invertebrate traits and functions into functional response groups (Laliberte & Legendre, 2010; Mumme et al., 2015; Villéger, 2008) and were contrasted with the paired savanna controls.

The final chapter (Chapter 6), discusses the main results from the previous chapters and attempted to place them in a broader context in order to gain a better understanding of the ecology of nutrient-hotspots in a relatively nutrient-poor savanna. Lastly, areas for future research were suggested.

CHAPTER 2

LITERATURE REVIEW

2.1 Historical ecology of abandoned kraals

All natural areas have a history, dating long time back with people who lived and worked with them. In African savannas, pastoralism has been one of the main economic activities practised in the last century (Du Toit & Cumming, 1999). Livestock farming then continued to face a myriad of challenges which led to a shift in land use and ultimately abandonment of livestock (Lindsey et al., 2013). In Africa, livestock ranching is being abandoned chiefly because its net gains are reducing while those of wildlife conservation are increasing (Kioko et al., 2012; Lindsey et al., 2013). For instance, in Kenya, Young et al, (1998) reported that optimal cattle production was expensive in the Laikipia District and shifted to conservation and eco-tourism. In the Associated Private Nature Reserve (APNR), South Africa, van der Waal et al, (2011) reported that livestock ranching was abandoned for wildlife conservation around 1970 mainly due to livestock diseases and poor market access. The Maasai herders of Tanzania are also abandoning pastoralism as they are facing challenges in land tenure as more land is needed for crop farming (Kioko et al., 2012). In Save Valley Conservancy, Zimbabwe, Lindsey et al, (2008) reported that cattle ranching was the main practice since 1972 (in the then Devuli and Humani Cattle Ranches) which was later abandoned in 1992 after an audit reported the profitability of wildlife conservation over cattle ranching. Cattle ranching became uneconomical due poor market-access, high prevalence of livestock diseases, depredation and incessant droughts (Waterhouse, 1994). In 1992, business was shifted to wildlife conservation and wild animals were re-introduced in 23 management units (former cattle ranches) under private ownership (Lindsey et al., 2008). In the process, the landscapes were left with unusually

nutrient-rich abandoned kraal sites which have become the long-term human footprint on natural areas with implications on the ecology of the natural ecosystem. Thus, understanding their natural history is essential part of conservation.

2.2 Abandoned kraals and nutrient heterogeneity

Savannas are heterogeneous systems characterised by landscapes of varying soil fertility levels (Du Toit et al., 2003; van der Waal, 2010). Nutrient-enriched habitat patches in tropical savannas are in the form of termite mounds (Joseph et al., 2014; Moe et al., 2009; Muvengwi et al., 2014), nutrient-rich geomorphological units (Grant & Scholes, 2006), abandoned human settlements (Muchiru et al., 2009; Söderström & Reid, 2010) and abandoned kraals (Porensky et al., 2013; van der Waal et al., 2011; Veblen & Young, 2010).

Influence of abandoned kraals on local soil fertility in the savanna ecosystem has been covered in many studies (Kizza et al., 2010; Muchiru et al., 2009; Porensky et al., 2013; Riginos et al., 2012; van der Waal et al., 2011; Veblen, 2012; Young et al., 1998). Abandoned kraal sites have significantly higher levels of soil nitrogen (N), phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) compared to the surrounding savanna landscape, suggesting to the effect of residual nutrients, continued deposition by herbivores and nutrient mineralisation (Kizza et al., 2010; van der Waal et al., 2011; Veblen, 2012). Soil fertility levels can be a factor of the kraal age chronosequence (Kizza et al., 2010; Veblen, 2012). For instance, Kizza et al., (2010) reported that soil N, P, K, Ca, Mg and sodium (Na) were initially low at early ages (1-5 years), peaked at 10-20 years and declined at 45 years on abandoned kraals in a semi-arid savanna in Botswana. Contrastingly, van der Waal et al. (2011) reported the same nutrients to be significantly higher on a 40 year old abandoned kraal with three times higher N-mineralisation rates than the savanna matrix plots in APNR, South Africa. Varying local edaphic characteristics can also yield different soil results. Veblen, (2012) recorded a decrease with age

of Mg (28%), Ca (28%) and Na (89%) on abandoned kraals on clay-rich 'black cotton soils' in Kenya. However in all reviewed studies (Kizza et al., 2010; Porensky et al., 2013; Riginos et al., 2012; van der Waal et al., 2011; Veblen, 2012), soil P levels remained high on abandoned kraals suggesting its ability to form stable insoluble mineral complexes at pH of 6 and 7 which minimises its leaching. Therefore, this study will validate these findings on 22-year old abandoned kraal sites found in predominantly granitic soils in a semi-arid savanna.

2.3 Abandoned kraals influence vegetation structure and composition

In natural ecosystems, the introduction of soil nutrient-rich patches ultimately leads to a direct or indirect change in plant community structure and composition (van der Waal, 2010). Plants respond to high soil fertility levels, thereby gaining a growth advantage than others in the same landscape (Veblen, 2012). Influence of soil nutrients on plant diversity can be explained by the Intermediate Disturbance Hypothesis (Connell, 1978; Huston, 2014) and the unimodal productivity-diversity hypothesis (Fraser et al., 2015; Grime, 1973). Plant species richness is expected to be maximum at intermediate soil fertility levels since at high and low soil nutrient levels, there is competitive exclusion of weaker species by naturally dominant species and environmental stress is high to limit plant establishment, respectively (Biswas & Mallik, 2010; Connell, 1978; Huston, 1979).

On nutrient-rich sites, plant density and structural attributes are high which deprive light and space for less competitive plants (Augustine et al., 2003; Schadek et al., 2009). It remains a debate whether productivity is a good predictor of plant species diversity (Fridley et al., 2012; Mittelbach et al., 2001; Tilman et al., 1997). For example, species richness had a negative relationship with increase in soil K, Ca, P and cation exchange capacity (CEC) suggesting lack of resources for natural competitors (Huston, 2000; Nadeau & Sullivan, 2015). Others demonstrated that plant diversity can increase substantially with increase in limiting soil

nutrients pointing to the increased ecosystem capacity to utilise nutrients thereby reducing nutrient loss through leaching (Augustine et al., 2003; Huston, 2014; Young et al., 2013).

It is also important to note that woody, grass and forb species respond differently to soil nutrients although little is known about this in African savannas. In tropical forests, Nadeau and Sullivan (2015) reported a significantly positive relationship between soil P, K, Ca, and Mg and forb species richness and a negative correlation with grass species richness. In African savannas, abandoned livestock areas are characterised by a higher density of herbaceous species than woody species (Augustine & McNaughton, 1998; van der Waal et al., 2011); dominance of a fewer naturally competitive woody species (Veblen, 2012), a short grass state and short secondary successional tree species (Veblen & Young, 2010). Low tree density is explained by constrained tree recruitment on fertile soils as competition with grasses is high (Grant & Scholes, 2006; van der Waal et al., 2011). On the other hand, herbivory has been invoked to explain the dynamics in plant community development on nutrient-enriched habitats (Adler et al., 2001; Marion et al., 2010; van der Waal et al., 2011; Veblen, 2012; Veblen & Young, 2010). For instance, herbivores are attracted to highly palatable forage and only select plants of a particular morphology with highest nutrient payoff thereby altering the competitive balance between functionally different growth forms (Adler et al., 2001; Veblen, 2012).

2.4 Abandoned kraals influence herbivory

Large ungulate herbivores are often attracted to nutrient-rich habitat patches which offers forage of high quantity and quality (Augustine et al., 2003; Grant & Scholes, 2006; Yessoufou et al., 2013). Plant species growing on nutrient-enriched habitats have been demonstrated to have higher levels of nutrients compared to those on the surrounding landscape. For example foliar nutrient concentrations were generally high on plants found on abandoned kraals (Muchiru et al., 2009; van der Waal et al., 2011), termite mounds (Holdo & McDowell, 2004; Muvengwi et

al., 2014), sodic sites (Grant & Scholes, 2006) and abandoned settlement areas (Schadek et al., 2009). Therefore, these areas serve as nutrient reserves for large ungulate herbivores in a relatively nutrient-poor habitat matrix, by providing them with sufficient N, P, K and Na essential for production during active growing stages (Augustine et al., 2003). Also, the nutrient hot-spots are reservoirs of greener and nutritious forage for grazers during the dry period when the palatability and nutrient levels of forage fall below the maintenance levels (Grant & Scholes, 2006; van der Waal, 2010).

Several studies conducted in African savannas attest that abandoned kraals are a foci of ungulate grazers and browsers in the dry season as evidenced by high deposition rates of dung and intense grazing pressure (Augustine et al., 2003; Muchiru et al., 2009; Porensky et al., 2013; Riginos et al., 2012; Treydte et al., 2010; van der Waal et al., 2011; Veblen & Young, 2010). For example, an experimental study done in APNR showed that on kraal sites, dung deposition was eight times higher and grazing 1.5 times higher than the control sites (van der Waal et al., 2011). Also, Augustine et al., (2003) reported that grazing pressure on abandoned kraals was significantly high (60% of Above Net Primary Production (ANPP)), being explained by high foliar P concentrations in grasses which met the requirements of lactating and pregnant ungulates. Other studies (reviewed in Riginos and Grace, 2008) suggest that the attraction of herbivores to abandoned kraals is in part explained by their anti-predator behaviour as they seek open areas (glades) with improved vigilance during night and day. In the long term, the relationship of herbivores and plants on abandoned kraals is thereby maintained by soil-plant-herbivore feedbacks as herbivores deposit huge amounts of nutrients through dung and urine, further enriching the soils and ultimately improve forage production (Augustine et al., 2003; van der Waal et al., 2011). Moreover, aboveground invertebrates are attracted to the high quality and quantity of vegetation and other organic substrates while the improved soil physio-chemical properties attracts belowground invertebrates which further increase the nutrient cycling rates

Although it is known that plant species respond differently to soil fertility levels (Nadeau & Sullivan, 2015), it is less clear how productivity and composition of forage species (grasses and forbs) found on abandoned kraals influence herbivory patterns.

2.5 Biodiversity response of macro-invertebrates to abandoned kraals

Given that varying levels of productivity on disturbed habitats alter the diversity of species and their functional roles (Decaëns et al., 1998; Hemerik & Brussaard, 2002; Laossi et al., 2008), it becomes more important to understand the diversity response of the more-sensitive guild of macro-invertebrates. Implications of habitat heterogeneity on African savannas has been well-researched, with much bias on large herbivores (Du Toit et al., 2003; Pretorius et al., 2011; Winnie et al., 2008). Despite the fact that invertebrates constitute the bulk of the biodiversity and serve as ecosystem engineers (Jones et al., 1994) and bio-indicators (Brussaard, 1997), their response to disturbance has received less attention in the African savannas (Warui, 2004).

Given that abandoned kraals are long-term nutrient-rich and productive habitat patches in a relatively dystrophic savanna landscape (Veblen & Young, 2010), their influence on macro-invertebrate assemblages is poorly known. A few studies available mainly focused on characterisation of better-known groups such as butterflies (*Lepidoptera*) (Wilkerson et al., 2013), ants (*Hymenoptera*) (Porensky et al., 2013) and spiders (*Araneae*) (Warui et al., 2004) and their identification limited to higher taxa. Invertebrate studies done in Kenya Long-term Exclosure Experiment (KLEE) reported that abandoned kraals (glades) elicit edge-effects on surrounding habitat with a complex, cascading ecological consequences on macro-invertebrate assemblages. For example, high density and abundance of *Acacia* ants was recorded inside glades and at glade edges (Porensky et al., 2013), high abundance of invertebrate food for birds found inside glades (Söderström & Reid, 2010) and contrastingly a decrease in *Calotis* spp. on herbivore-excluded plots (Wilkerson et al., 2013). Elsewhere, macro-invertebrate richness was

found to be positively correlated to limiting soil N, P and K (Doblas-Miranda, Sánchez-Piñero, et al., 2009; Wu et al., 2015) and plant richness and composition (Haddad et al., 2001) suggesting the role of soil fertility in determining the quality and quantity of feed resources as a key factor for the establishment of macro-invertebrates.

On the other hand, above and belowground macro-invertebrate communities respond differently to resource heterogeneity (Doblas-Miranda, et al. 2009; Wardle et al. 2004; Vandegehuchte et al. 2011). For example, aboveground macro-invertebrates are much influenced by plant and litter properties, whereas belowground macro-invertebrates are affected by soil mineral properties (Doblas-Miranda, et al. 2009).

Recently, the use of functional diversity as a measure of biotic changes after disturbance has gathered momentum. According to Petchey and Gaston (2006), functional diversity is a powerful tool for predicting ecosystem functioning (stability and resilience) after a disturbance using the organisms' behavioural and morphological traits directly linked to a particular function. However, very few of such studies are available in African savannas. It is important to note that functional and taxonomic diversity response of macro-invertebrates may differ within the same community owing to the presence or absence of functionally redundant species (Laliberte et al., 2010). Other studies (Audino et al., 2014; Barragan et al., 2011) found contrasting results on taxonomic richness and functional dispersion and evenness, whereas Mumme et al. (2015) reported the alteration of both taxonomic and functional diversity in the tropical forest of Indonesia.

CHAPTER 3

Influence of abandoned cattle enclosures on plant assemblages and herbivory in a semi-arid savanna. *

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Abstract

In semi-arid savannas, abandoned cattle (*Bos taurus*) enclosures or kraals have been demonstrated to be nutrient-hotspots for large herbivores. In this study, we examined the interaction between herbivory and forage quality, structure and diversity at 12 kraals (abandoned for 22 years) paired with savanna control plots in Save Valley Conservancy, Zimbabwe. Plant diversity was not different between sites. Herbaceous cover was higher and woody species density lower on abandoned kraals than control plots. Furthermore, abandoned kraals had higher herbaceous productivity and foliar nutrient concentration for grasses than forbs. The abandoned kraals had higher concentration of soil nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), sodium (Na), organic carbon (C) compared with control plots and a slightly acidic pH. Grasses were grazed more than forbs on nutrient-rich abandoned kraals. Only herbaceous biomass for grasses had a significant influence on the interaction between plants and herbivory. No clear relationships were observed between forage quality and herbivory and plant species diversity. Abandoned kraals provide patches of nutrient-rich forage, increasing savanna heterogeneity and in turn influence grazing patterns of large herbivores, and therefore influence ecosystem functioning. A conservation monitoring programme is recommended on such nutrient-rich patches as they serve as foraging-hotspots for herbivores in a dystrophic African semi-arid savanna.

Keywords: Abandoned kraals; Diversity; Forage quality; Herbivory and nutrient-hotspots

3.1 Introduction

Savanna vegetation heterogeneity is shaped by both biotic and abiotic factors which operate at different spatio-temporal scales (Du Toit et al., 2003; Sankaran et al., 2005; Scholes & Archer, 1997). At global scale vegetation heterogeneity (composition and structure) is mainly determined by climate (temperature and precipitation) (Sankaran et al., 2005), with fire and

herbivory becoming more important at regional to landscape scales (Asner et al., 2009; Bond et al., 2005). Geological variation was observed to be an important source of vegetation heterogeneity within landscapes (Grant & Scholes, 2006; Muvengwi et al., 2017) whereas fine spatial scale vegetation heterogeneity has been attributed to dung beetles (*Coleoptera*) (Andresen, 2003), latrines (Pouvelle et al., 2016), beavers (*Castor fiber*) (Wright et al., 2016), termites (*Isoptera*) (Holdo & McDowell, 2004; Muvengwi et al., 2014) and abandoned kraal sites (Porensky & Veblen, 2015; van der Waal et al., 2011).

In African savanna ecosystems, the periodic conversion of cattle (*Bos taurus*) ranches and livestock pastures into conservation areas has left persistently nutrient-rich patches enriched with dung and urine. Plant productivity and forage quality have been reported to be higher at former kraal sites compared to the expansive landscapes where they occur (Veblen, 2012). Hence, kraal sites attract foraging large mammalian herbivores that in turn maintain high nutrient levels through a positive feedback loop when they drop their dung and urine (Augustine et al., 2003; van der Waal et al., 2011). However, some studies in the savannas contended the general observation that nutrient-rich patches are always foraging hotspots for herbivores (Muvengwi et al., 2013; van der Plas et al., 2013), an observation that is attributed to environmental context, where fewer differences in soil nutrients between the nutrient hotspots and the surrounding environment may occur (O'Connor, 2013). This observation calls for more empirical studies before generalisations of the effect of nutrient hotspots are made.

Over the last two decades, considerable research effort has been focused on abandoned cattle enclosures, with the aim of understanding how they influence soil, large mammalian herbivory and plant species diversity (Muchiru et al., 2009; Porensky & Veblen, 2015; Riginos et al., 2012; van der Waal et al., 2011; Veblen, 2012; Young et al., 1998). Soil nutrients have been demonstrated to have a strong positive relationship with forage quality (Grant & Scholes, 2006;

Holdo & McDowell, 2004). For instance, several studies reported twice as high foliar nitrogen and phosphorus on nutrient-rich sites compared with the surrounding savanna landscape (Augustine et al., 2003; Muchiru et al., 2009; van der Waal et al., 2011; Veblen, 2012). This has been suggested as a major factor why large herbivores preferentially graze on nutrient-rich sites (Augustine et al., 2003). For example, impala (*Aepyceros melampus*) and blue wildebeest (*Connochaetes taurinus*) grazed more on sodic sites (Grant & Scholes, 2006), zebra (*Equus quagga)* and waterbuck (*Kobus ellipsiprymnus*) on termite mounds (Mobaek et al., 2005) and elephants (*Loxodonta africana*) on fertilised mopane (*Colophospermum mopane)* plots (Pretorius et al., 2011).

Different foraging habits and feed preference of large herbivores may influence the dynamics among plant species assemblages (Joseph et al., 2013; van der Waal et al., 2011). During feeding, herbivores tend to select the most conspicuous and palatable plant species thereby causing contrasting effects on growth and dominance of forage species (Adler et al., 2001; Augustine & McNaughton, 1998). It has been hypothesised that grasses are more preferred than woody or forbs on nutrient-rich sites despite yielding lesser nutrient content than the later owing to the defensive compounds found in most forb and woody species (Du Toit et al., 2003; Owen-smith & Cooper, 1987; van der Waal, 2010). To date, several studies have attempted to demonstrate the relationship between forage properties and herbivory on abandoned kraals (reviewed in Riginos et al. 2012; Porensky and Veblen 2015) but with varying findings owing to different environmental contexts and site age.

In order to understand the effect of abandoned kraal sites on herbivory, forage quality and vegetation structure and composition, we sampled vegetation growing on kraal sites and the surrounding savanna matrix (hereafter control plots). The specific objectives of the study were to: (i) test whether soil enriched by cattle dung and urine (during cattle ranching era) and later

by soil-plant-herbivore feedback loop (van der Waal et al., 2011) is still detectable in soil after 22 years of abandonment, (ii) assess whether abandoned kraals as sources of habitat scale heterogeneity are influencing vegetation structure and composition, (iii) determine whether abandoned kraals (22 years later) are still areas of high plant productivity and provide nutrient-rich forage, and (iv) assess the relationship between grazing by large mammalian herbivores and forage quality, structure and composition. We hypothesised that abandoned kraals are still nutrient-rich patches affecting vegetation structure and composition and ultimately large mammalian herbivory.

3.2 Materials and Methods

3.2.1 Study area

The study was conducted in the Save Valley Conservancy, south-eastern lowveld of Zimbabwe (20° 05´ S, 32° 00´ E) which covers an area of about 3,387 km^2. Since 1925, the area was used for large scale cattle ranching with an estimated maximum herd of 24,000 cattle in 1975 (Lindsey et al., 2008). The cattle ranching was heavily affected by cattle theft which reduced the herd to 5,000 in 1979 and the 1991–1992 drought which forced ranchers to sell all the cattle (Lindsey et al., 2008). By 1992, cattle ranching was abandoned and business shifted to wildlife conservation (Waterhouse, 1994). The area lies in the savanna semi-arid zone with annual rainfall ranging from 300 to 500 mm (Lindsey et al., 2008). The geology consists largely of gneisses and paragneisses forming gently, undulating terrain with scattered kopjes. Vegetation is mainly deciduous open woodland savanna with four major woodlands types which are kopje, riverine thicket, mopane and *Combretum* open and scrub mopane (Waterhouse, 1994). Herbaceous community is dominated by a mixture of annual and perennial grasses such as *Setaria*, *Panicum* and *Cenchrus* species. Among its diverse wildlife species, there is: elephant, buffalo (*Syncerus caffer*), leopard (*Panthera pardus*), lion (*Panthera leo*), black rhinocerous

(*Diceros bicornis*), white rhinocerous (*Ceratotherium simum*) and other ungulate herbivores including Burchell's zebra, giraffe (*Giraffa camelopardalis*), impala, sable antelope (*Hippotragus niger*) and hippopotamus (*Hippopotamus amphibius*).

3.2.2 Selection of sampling plots

Twelve kraals, abandoned for 22 years (year 1992 to 2014) were chosen as sampling plots. All the kraals were found with a measurement of 100 m × 100 m (a standard kraal size of the then Devuli cattle ranch). Each kraal was used to accommodate about 400 beasts during the night. To correctly identify the locations of the kraals, we engaged a former cattle herder who worked in the conservancy during the cattle ranching era. Remnant features like water troughs, fencing posts and management roads helped us confirm the exact location of the kraals. Similar-sized control plots were marked 200 m from the mid-point of each selected kraal at the same topographical level minimising soil and topography variations following a protocol used by van der Waal et al. (2011). Sampling was done in the wet season (November 2014 to April 2015) when savanna vegetation has leaves and easy to identify (Walker, 1976).

3.2.3 Soil sampling and chemical analyses

In each sampling plot, five samples were randomly collected using a soil auger to a depth of 15 cm (the herbaceous vegetation primary rooting zone) and thoroughly mixed to obtain a composite sample. Soil samples were chemically analysed for available phosphorus (P), mineral nitrogen (N), extractable potassium (K), exchangeable calcium (Ca), sodium (Na) and magnesium (Mg), organic carbon (C) and pH. Analysis of the soil properties was based on standard laboratory techniques on soil analyses (Anderson & Ingram, 1993; Motsara & Roy, 2008). Mineral N was determined by micro-Kjeldahl digestion followed by distillation, available P was measured spectrophotometrically following the Olsen's method and extractable

K by a flame photometry (Motsara & Roy, 2008). Exchangeable cations (Ca, Mg and Na) were extracted with ammonium acetate and then measured using atomic absorption spectrophotometry (Anderson & Ingram, 1993). Soil pH was measured using water and $CaCl_2$ suspension and Organic C was determined volumetrically following procedures described by Motsara and Roy (2008). All laboratory soil analyses were conducted at the Chemistry and Soil Research Institute, Ministry of Agriculture, Mechanisation and Irrigation Development, Harare, Zimbabwe.

3.2.4 Vegetation sampling

Woody vegetation structure and composition was assessed in 100 m × 100 m plots following the same procedures described in Gandiwa et al. (2011). For herbaceous vegetation structure and composition, quadrats (1 m × 1 m) were placed (10 m apart) along each of the nine selected 100 m transects per plot. All plants encountered were identified to species level and recorded against their relative abundances.

Herbaceous biomass (aboveground) was determined for each sampling plot by measuring the compressed height with a disk pasture meter (calibrated for Lowveld vegetation) dropped twice in every quadrat. Biomass was then calculated using the same equation of Trollope, (1990) as follows:

$$Biomass\ (kg\ ha^{-1}) = (\sqrt{X} \times 2260) - 3019$$

Where X is the average disk height for the sampling plot.

Basal and aerial cover estimations followed the 8-point scale by Walker, (1976) and every species found within the quadrat was recorded along with the sum cover of that species (Manier & Hobbs, 2007).

The level of grazing was assessed using the degree of defoliation of herbaceous tufts (Grant & Scholes, 2006). Tuft utilisation assessment was done for every species found in a quadrat and an estimated grazing percentage was recorded. Care was taken not to account for defoliation not related to grazing. Percentage tuft utilisation was calculated from the ratio of utilised tufts over total number of tufts (Grant & Scholes, 2006).

Foliar nutrient analyses were done for the commonly found plant species in paired kraal-control plots. Leafy material of commonly found species (trees: mopane, *Grewia bicolor* and *Acacia tortilis*; forbs: *Sida alba*, *Solanum incanum* and *Vernonia myriantha* and grasses: *Urochloa mosambicensis*, *Panicum maximum* and *Chloris virgata*) was randomly collected and oven-dried at 70 °C and milled with a 0.5 mm sieve. Chemical analyses were done for nitrogen (N), phosphorus (P), potassium (K), magnesium (Mg), calcium (Ca), iron (Fe), manganese (Mn), zinc (Zn) and boron (B) using standard procedures described in Motsara and Roy (2008).

3.2.5 Data analyses

Data were first tested for normality using Shapiro-Wilk test in the Paleontological Statistics Software package (PAST) (Hammer, 2009) and all non-normal, percentage and concentration data were transformed as necessary to improve data distribution. All comparisons between abandoned kraals and controls were done using paired *t* tests in Statistical Package for Social Scientist (SPSS) version 21 (IBM Corporation, 2012). Shannon's diversity index (*H´*), Whittaker's beta diversity (β_w) and Sørensen's similarity index were assessed at plot level (Nishizawa et al., 2016). The relationship between levels of grazing and forage quality, as well as the relationship between forage quality and soil conditions was analysed using Pearson's correlation analysis. Further, we performed simple linear regression analysis to determine the relationship between soil conditions (dependant variables) and plant diversity indices

(dependant variables) following Huang et al. (2013). To explore how environmental factors (grazing, foliar and soil nutrient concentration and herbaceous productivity) influence grass and forb species composition, we used multivariate ordination analyses. A constrained ordination Canonical Correspondence Analysis (CCA) with the CANOCO 4.5 package was applied (Lepš & Smilauer, 2003).The unimodal CCA was selected because the first axis of the Detrended Correspondence Analysis (DCA) of the data set had a gradient length equal to 5.64 standard deviation units (Lepš & Smilauer, 2003). Infrequent species (with abundances <0.5%) were eliminated and abundances were $\log_{10}$ transformed (Lepš & Šmilauer, 1999). Significance of axes and environmental variables were tested by Monte Carlo tests (999 permutations) and ordination diagrams were constructed for the first and second axes.

3.3 Results

3.3.1 Influence of abandoned kraals on soil characteristics

Concentrations of soil mineral N, available P, K and extractable Ca were significantly higher on abandoned kraals with factors 1.73, 1.44, 2.59 and 1.32 respectively. Soil pH was more slightly acidic on control plots than abandoned kraals (P = 0.012). Although location showed no significant effect on concentrations of extractable Mg, Na and organic C, concentrations were on average higher on abandoned kraals (Table 1).

Table 1. Comparisons of soil nutrients between abandoned kraals and control plots in Save Valley Conservancy, (mean ± standard error, N = 12).

Soil variable	Kraal	Control	***t***	***P***
Mineral N (ppm)	29.40 ± 2.71	17.00 ± 1.75	3.70	**0.003**
Avail. P (ppm)	42.92 ± 3.97	29.83 ±2.49	3.08	**0.010**
pH ($CaCl_2$)	5.30 ± 0.13	4.66 ± 0.20	2.96	**0.012**
Ex Ca (me%)	2.08 ± 0.15	1.58 ± 0.14	3.07	**0.011**

Ex Mg (me%)	1.15 ± 0.12	1.03 ± 0.15	0.58	0.569
Ex Na (me%)	0.24 ± 0.02	0.23 ± 0.02	0.19	0.849
Ex K (me%)	0.88 ± 0.16	0.34 ± 0.04	3.09	**0.010**
Organic C (%)	1.47 ± 0.61	1.01 ± 0.39	0.52	0.609

Significant P-values (P < 0.05) are shown in bold

3.3.2 Influence of abandoned kraals on vegetation structure and composition

No significant differences (P > 0.05) in species diversity (Shannon-Wiener) for woody, forbs and grasses were recorded (Table 2). However, species richness of woody plants and evenness of forbs differed significantly (P < 0.05) between abandoned kraals and control plots with the higher values recorded for controls. Vegetation cover (basal and aerial) for both forbs and grasses was significantly higher (P < 0.05) on abandoned kraals than control plots. Although woody structure was similar in both sites (P > 0.05), density was significantly higher (P < 0.05) on control plots (Table 2).

Table 2. Comparisons of vegetation structure and composition between abandoned kraals and control plots in Save Valley Conservancy, (mean ± standard error, *N*= 12).

Vegetation composition				
Grasses	**Kraal**	**Control**	***t***	***P***
Richness	5.00 ± 0.69	4.67 ± 0.47	0.13	0.901
Evenness	0.58 ± 0.06	0.65 ± 0.05	-1.51	0.158
Shannon diversity (H´)	1.03 ± 0.17	1.18 ± 0.09	-1.47	0.169
Forbs				
Richness	7.00 ± 0.66	5.75 ± 1.03	1.44	0.177
Evenness	0.54 ± 0.03	0.75 ± 0.05	4.67	**0.007**
Shannon diversity (H´)	1.49 ± 0.10	1.35 ± 0.17	1.03	0.324
Woody				
Richness	4.50 ± 0.57	7.25 ± 0.77	-3.35	**0.007**
Evenness	0.61 ± 0.05	0.47 ± 0.05	2.07	0.063

Shannon diversity (H´)	1.07 ± 0.17	1.38 ± 0.16	-1.61	0.136
Vegetation structure				
Grasses				
Basal cover (%)	9.66 ± 2.06	5.57 ± 1.65	2.70	**0.021**
Aerial cover (%)	25.62 ± 6.53	13.19 ± 3.90	2.82	**0.017**
Forbs				
Basal cover (%)	1.50 ± 0.19	0.67 ± 0.10	4.83	**0.001**
Aerial cover (%)	5.86 ± 0.84	3.26 ± 0.46	3.03	**0.011**
Woody				
Height (m)	5.57 ± 0.61	5.51 ± 0.38	-0.13	0.899
Basal area (m^2)	0.04 ± 0.01	0.04 ± 0.01	-0.14	0.890
Canopy volume (m^3)	27.33 ± 8.36	14.38 ± 1.76	1.00	0.339
Density (ha^{-1})	0.12 ± 0.01	0.28 ± 0.03	-5.12	**<0.001**

Significant P-values (P < 0.05) are shown in bold.

3.3.3 Influence of abandoned kraals on herbaceous productivity and herbivory

Abandoned kraals yielded a significantly higher (*P* = 0.036) herbaceous biomass (aboveground) than the controls (Fig. 2a). Grasses on abandoned kraals were significantly grazed (*P* = 0.025) than on control plots while grazing percentage for forb species was not significantly different (*P* = 0.082) between sites (Fig. 2b).

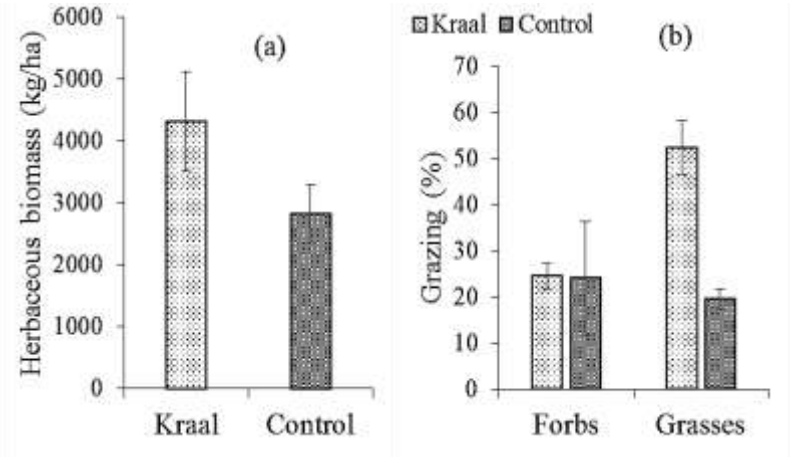

Figure 2. Herbaceous biomass (aboveground) and grazing percentage estimation (mean ± standard error) for forb and grass species between abandoned kraals and controls in Save Valley Conservancy.

3.3.4 Influence of abandoned kraals on foliar nutrient concentration

Abandoned kraals supported grasses with significantly higher concentrations of foliar N, P, K, Ca, Mg, Fe, Mn, Zn and B with factors 1.21, 1.67, 1.28, 1.29, 1.43, 1.23, 1.42, 1.70 and 1.49 respectively (Fig. 3a-i).

Unlike grasses, forbs showed a similar concentrations of foliar nutrients with the exception of K which was 1.33 times higher ($P = 0.023$) on abandoned kraals (Fig. 3c). Woody species found on abandoned kraals had higher ($P < 0.05$) concentrations of foliar K, Mg, Mn and B with factors 1.33, 1.53, 1.36 and 1.31 respectively (Fig. 3c, e, g and i).

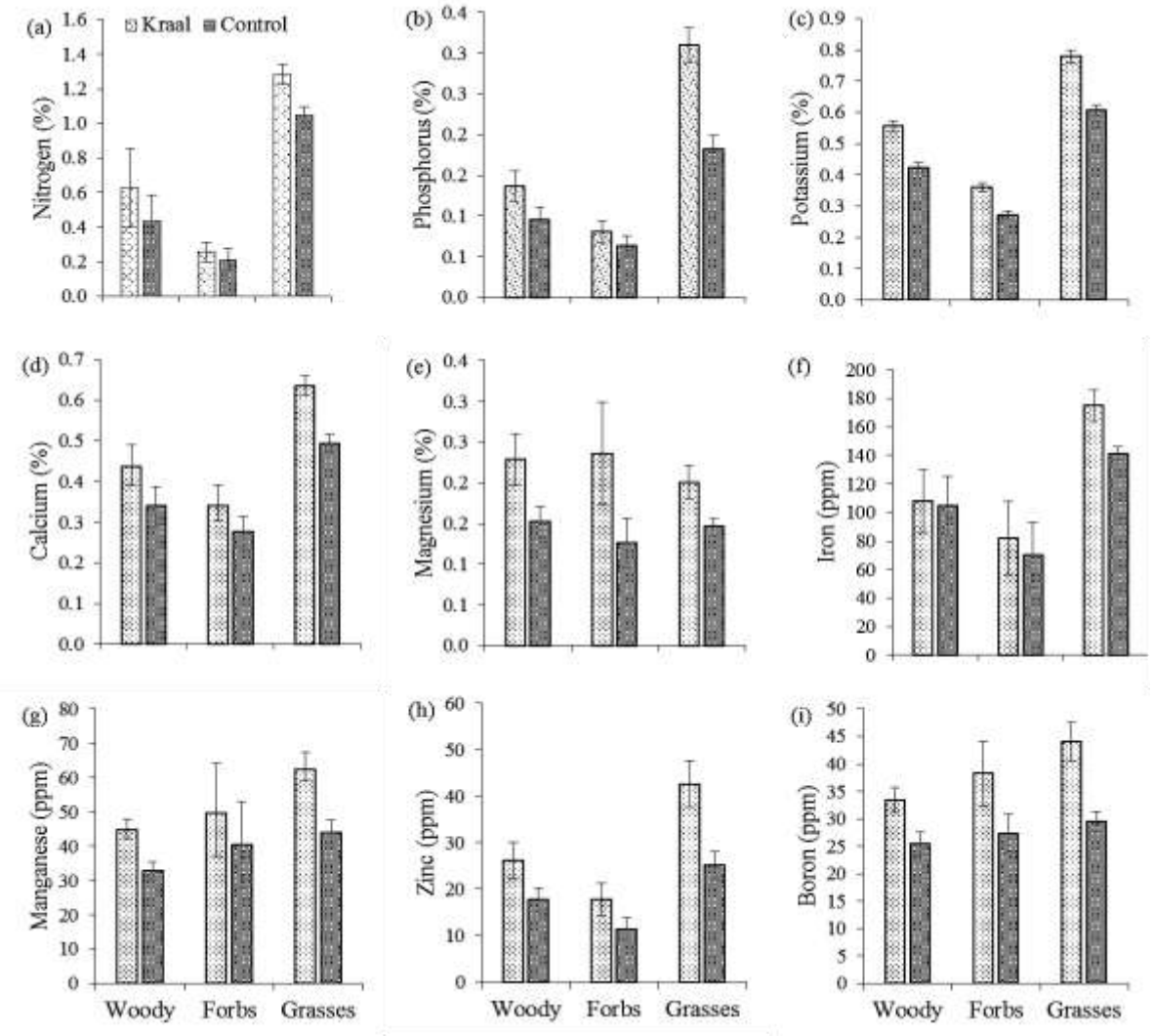

Figure 3. A kraal-control comparison of foliar nutrient concentrations (mean ± standard error) of commonly found trees (*C. mopane, G. bicolor and V. tortilis*), forbs (*S. alba, S. incanum and V. myriantha* and grasses (*U. mosambicensis, P. maximum and C. virgata)*.

3.3.5 Relationship of forage species community to environmental factors

3.3.5.1 Grasses

The results of the CCA showed that the first axis accounted for 47% of the variance. The species-environment correlations for the two axes were high (Table 3). The first axis explained 32.9% of the variation (Monte Carlo permutation test, *F*-ratio = 2.17, *P* = 0.038). The permutation test showed that biomass explains a significant proportion of the species assemblages. Also, the small angles between the arrows for N, P, K, Gr% (grazing percentage) and Bm (biomass) indicate a positive correlation between those variables and forage species. Explanatory variables; BC, SW, Gr% and P showed no significant influence on the structure and composition of forage species (Fig. 4; Table 3).

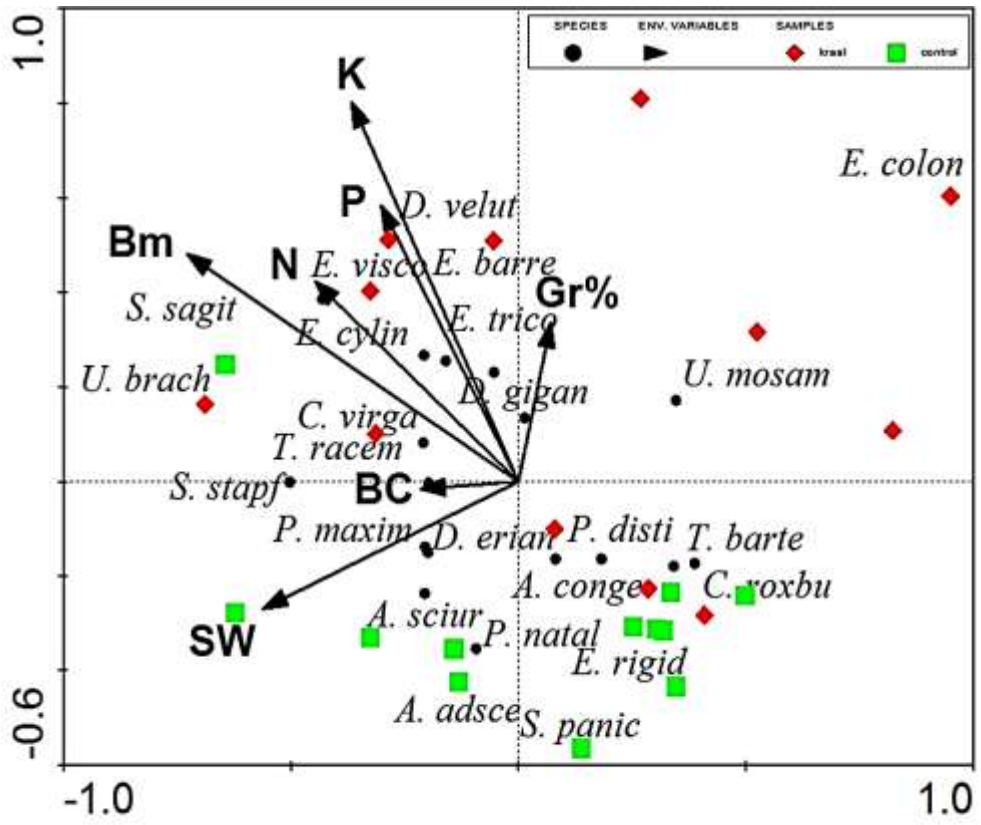

Figure 4. Canonical Correspondence Analysis triplot for grass species and environmental variables from abandoned kraals and control plots in Save Valley Conservancy, Zimbabwe. Environmental variables: N: Nitrogen; P: Phosphorus; K: Potassium; BC: Basal cover; Bm: Biomass; Gr%: Grazing percentage and SW: Shannon-Wiener diversity. Grass species: *E. colon. Eragrostis colona; D. velut. Digitaria velutina; E. visco. Eragrostis viscosa; E. barre. Eragrostis barrelieri; S. sagit. Setaria sagittifolia; U. brach. Urochloa brachyuran; E. cylin. Eragrostis cylindrifolia; E. trico. Eragrostis tricophora; D. gigan. Dactyloctenium gigangteum; C. virga. Chloris virgata; T. racem. Tragus racemosa; U.mos. Urochloa mosambicensis; S. stapf. Sporobolus stapfianus; P. max. Panicum maximum; D. erianth. Digitaria eriantha; P. dist. Panicum distichum; T. barte. Tragus barteronianus; A.conge. Aristida congesta; C. roxb. Chloris roxburghiana; A. sciur. Aristida sciurus; P. natal. Panicum natalense; E. rigidior. Eragrostis rigidior; A. adsce. Aristida adscensionis* and *S. panic. Sporobolus panaicoides*

Table 3. Ordination CCA results for the first two axes for grasses (Fig. 4) and forbs (Fig. 5) and environmental variables on abandoned kraals and control plots in Save Valley Conservancy, Zimbabwe.

	Grasses			**Forbs**		
	Axis 1	**Axis 2**	**P-value**	**Axis 1**	**Axis 2**	**P-value**
Eigenvalues	0.47	0.34		0.41	0.28	
Variance explained (%)	32.90	53.90		32.40	54.40	
Cumulative variance (%) by axis	53.90	86.80		54.40	86.90	
Intra-set correlation coefficients						
Biomass	-0.56	-0.27	0.034	0.21	-0.42	0.092
Mineral N	-0.73	0.48	0.682	0.49	-0.31	0.763
Available P	-0.21	-0.02	0.975	0.31	0.03	0.428
Extractable K	0.07	0.34	0.942	0.30	0.29	0.461
Basal cover	-0.45	0.42	0.465	0.68	-0.06	0.636
Grazing (%)	-0.30	0.58	0.753	-0.11	-0.53	0.414
Diversity (Shannon-Wiener)	-0.37	0.80	0.058	-0.60	-0.69	0.509

3.3.5.2 Forbs

The first two axes for the CCA for forbs (F-ratio = 1.79, P = 0.276) and all other axes combined (F-ratio = 1.03, P = 0.368) explained the variation of the data although they were not statistically different (Table 3).Although no clear separation of samples (kraals and controls) was observed, all the axes had species-environment correlations greater than 0.6 (Fig. 5). The first axis had a moderately strong negative species-environment correlation (r = –0.686) and represents a gradient of decreasing diversity (SW) associated with *B. pilosa* (highest score). The second axis represent a gradient of increasing basal cover (r = 0.682) with an association

with *A. hispidium*. All explanatory variables had a non-significant relationship with forb species and biomass while soil N, P and K had very weak correlations with both axes (Table 3).

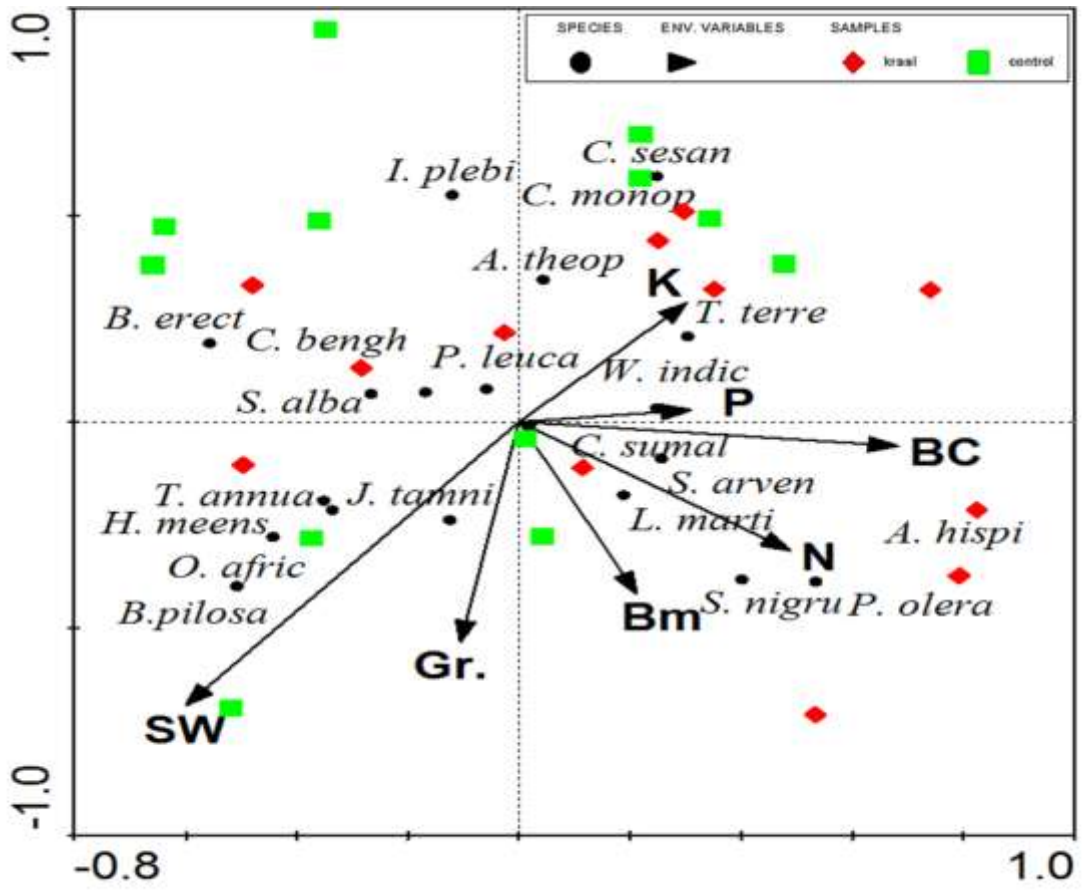

Figure 5. Canonical Correspondence Analysis triplot for forb species and environmental variables from abandoned kraals and control plots in Save Valley Conservancy, Zimbabwe. Environmental variables: N: Nitrogen; P: Phosphorus; K: Potassium; BC: Basal cover; Bm: Biomass; Gr: Grazing percentage and SW: Shannon-Wiener diversity. Forb species: *C. sesan*. *Ceratotheca sesanoides*; *I. plebi*. *Ipoemia plebia*; *C. monop. Cleome monophyla*; *A. theop. Abutilon theophrasti*; *T. terre. Tribulus terrestris*; *B. erect. Boerhavia erecta*; *C. bengh. Commelina benghalensis*; *P. leuca. Phyllanthus leucanthus*; *W. indica. Waltheria indica*; *S. alba. Sida alba*; *C. sumal. Conyza sumaltensis*; *T. annua. Triumfeta annua*; *J. tamni. Jacquemontia tamnifolia*; *S. arven. Spergula arvensis*; *H. meens. Hibiscus meensii*; *L. mart. Leucas martinicensis*; *A. hispi. Acanthospermum hispidum*; *B. pilosa. Bidens pilosa*; *S. nigru. Solanum nigrum* and *P. olera. Portulaca oleracea*.

3.4 Discussion

Our results showed that abandoned kraals were still nutrient-rich after 22 years of abandonment with a high production of nutritious grass plants preferred by herbivores. Surprisingly, among the forage species, the dominant forb species on abandoned kraals were least consumed by herbivores and showed higher foliar nutrient concentrations between kraals and controls. Contrary to the present study, plant diversity did not respond to abandoned kraals and plant cover was less important in explaining the plant community composition. Plant diversity had a negative relationship with grazing and forage quality.

Soil nutrient levels were high on abandoned kraals than control plots suggesting the persistence of nutrients a long time after abandonment. These findings corroborate other studies done on abandoned kraals in the savannas (Kizza et al., 2010; Porensky et al., 2013; van der Waal et al., 2011). Soil nutrients on nutrient hotspots has been reported to be largely maintained by a positive feedback loop whereby herbivores feeding on them drop dung and urine in the process further enriching the sites (Augustine & McNaughton, 2006; van der Waal et al., 2011). For instance, in this study the limiting soil nutrients N, P, K, and Ca were much higher on abandoned kraals than control plots.

Previous studies have demonstrated that grazing on nutrient-rich patches may alter the trends in plant community structure and composition (Manier & Hobbs, 2007; Riginos et al., 2012; Young et al., 2013). We recorded that nutrient-rich forage found on abandoned kraals and the subsequent increased grazing were not associated with changes in alpha and beta diversity of grass, forb and woody species. However, our results must be treated with caution since we did not use exclosure plots on kraals. These findings are contrary to the productivity-diversity hypothesis whereby plant diversity was supposed to be lower on nutrient-rich abandoned kraals likely due to the competitive exclusion by fewer dominant species (Grime, 1973). Other studies

have concluded that plant diversity increases with high grazing on nutrient-rich habitats and decreases in nutrient-poor habitats (see Okullo and Moe, 2012). According to the grazer-reversal hypothesis (Proulx & Mazumder, 1998), diversity increases with high grazing on nutrient-rich habitats and decreases under nutrient-poor conditions. A lower plant diversity on nutrient-rich habitats compared to the surrounding matrix has been recorded by others in the savannas (Okullo & Moe, 2012; Porensky et al., 2013; Porensky & Veblen, 2015; Veblen & Young, 2010) suggesting the dominance of a fewer competitive forb species over grasses on nutrient-rich areas. We also suggest that after two decades plant species mix could have been achieved through seed dispersal via ungulates and birds.

A lower woody species density on abandoned kraals points to the constrained establishment of woody species in a grass dominated habitat (Scholes & Archer, 1997; van der Waal, 2010) and probably the destructive mechanical clearance of vegetation done during setting up of kraals. However, woody height, basal area and canopy volume were similar between sites mainly because their means were skewed by extreme values of remnant large trees left inside kraals. An increase in productivity of herbaceous plants (grasses and forbs) on abandoned kraals can be attributed to their competitive growth advantage over woody species on areas of high soil fertility and increased sprouting of annuals during the wet-season (van der Waal, 2010). Elsewhere, forbs and graminoids have been reported to dominate nutrient-rich habitats such as termite mounds (Okullo et al., 2013) and abandoned pastoral settlements (Muchiru et al., 2009).

Herbaceous biomass and plant cover were twice as high on abandoned kraals perhaps showing the positive response of herbaceous plants to limiting soil nutrients in semi-arid savannas (Veblen & Young, 2010). A higher concentration of foliar nutrients for grasses on abandoned kraals compared to the same species in the matrix, suggest why herbivory was high on abandoned kraals. According to optimal foraging strategies, herbivory is much influenced by

the quality and quantity of forage (Owen-Smith and Cooper 1987; Grant and Scholes 2006). Regardless the smaller size of kraals (100 m × 100 m) compared to the matrix, herbivores preferred feeding on these sites perhaps because they supported high quantity and nutritious forage. Perhaps, forb species were not as much preferred as grass species on abandoned kraals probably because of their greater chemical defence or lower nutritional returns to animals (Ball et al., 2001; Du Toit et al., 2003). This result is in line with the findings of Riginos and Grace, (2008) who recorded a decreased consumption of forbs despite higher protein levels than grasses.

Results from the CCA for grasses indicated that herbaceous biomass is an important factor explaining the differences in plant structure and composition between abandoned kraals and control plots. However, others have demonstrated that nutrient-rich sites are usually dominated by plant monocultures which yield a high biomass per unit area (Laossi et al., 2008; Veblen, 2012). Considering CCA results for forbs, no obvious pattern was evident between measured explanatory variables and forb species in both sites pointing to the unresponsive nature of forbs to soil fertility levels and poor grazing preference by herbivores (Ball et al., 2001; Du Toit et al., 2003). In contrast to our study hypothesis, results showed that grazing had a non-significant relationship with grass communities whereas species diversity had a negative relationship with both grass and forb communities. This result might be explained by the existence of most palatable and acceptable grasses recorded in this study which could perhaps reduce feed selectivity by herbivores (Augustine & McNaughton, 1998). It is important to note that unlike the highly preferred grass species, forb species respond differently to herbivory on abandoned kraals.

3.5 Conclusion

This study adds to the current available knowledge of an ecosystem in a previously disturbed conservation area which has been left with remnant nutrient-rich patches. Residual soil nutrients were still higher on kraals, perhaps being maintained by plant-herbivore-soil nutrient feedbacks. Abandoned kraals harbour grass forage of high quality which is more utilised by herbivores. Utilisation of forage was more explained by foliar nutrient concentrations and herbaceous productivity than plant diversity. Among the forage species, forbs had low foliar nutrient concentration and were less preferred by herbivores at least in the rainy season. Future studies should therefore explore the spatio-temporal links between herbivory of forbs and graminoids on nutrient-hotspots in semi-arid savannas and elsewhere in an exclusion experiment. We recommend a conservation monitoring programme on abandoned kraals as they are serving as nutrient-hotspots for herbivores in an otherwise dystrophic semi-arid savanna.

3.6 Acknowledgements

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CHAPTER 4

Diversity and abundance of macro-invertebrates on abandoned cattle (*Bos taurus*) enclosures in a semi-arid savanna*

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Abstract

Abandoned cattle (*Bos taurus*) kraals are sources of habitat heterogeneity in dystrophic semi-arid African savannas with a strong influence on soil nutrients and plant productivity. However, little is known regarding how improved soil nutrients and plant productivity influence soil macro-invertebrate assemblages on the disturbed habitat. We tested whether two surrogates of productivity (herbaceous biomass and soil nutrients) have an effect on aboveground and belowground macro-invertebrate assemblages. Twelve abandoned kraals were contrasted with their paired control plots for soil characteristics, herbaceous productivity and macro-invertebrate assemblages in Save Valley Conservancy, Zimbabwe. Abandoned kraals had significantly higher concentrations of soil nitrogen (N), phosphorus (P), potassium (K) and calcium (Ca) as well as herbaceous biomass, basal and aerial cover than control plots. Species richness was significantly high on abandoned kraals. Only the belowground invertebrate diversity (Shannon *H′* and Hill N1) responded significantly to the influence of abandoned kraals. Soil nutrients and herbaceous productivity had positive and significant correlations with the dominant taxa (Coleoptera, Hymenoptera, Hemiptera, Isoptera and Myriapoda) on abandoned kraals. Results suggest that kraals exert strong forces on savanna spatial heterogeneity, with implications on ecosystem processes and functioning.

Keywords: macro-invertebrates; nutrient heterogeneity; productivity-diversity hypothesis; nutrient hotspots; abandoned kraals

4.1 Introduction

The productivity-diversity hypothesis was postulated long back (Grime 1973), and has been tested on a variety of taxa (Šímová et al. 2013; Hawkins et al. 2003; Owen 1988). Under this hypothesis high species diversity is expected at intermediate levels of productivity, since environmental stress and competition limits diversity at the low and high extremes of productivity (Grime, 1973; Huston, 1979; Mittelbach et al., 2001). At low productivity levels, species diversity is limited by environmental stress such as insufficient mineral nutrients and water which few species are able to tolerate whereas at high productivity levels species diversity is constrained by competitive exclusion by few dominant species (Fraser et al., 2015). Two forms of productivity-diversity relationships have been proposed and these are, unimodal (hump-shaped) and monotonic (Abrams, 1997). In an extensive review of over two hundred empirical studies, about 45% of the studies on vascular plants had a hump-shaped relationship while no obvious pattern was observed for animals (Mittelbach et al., 2001). Furthermore, there is no clear relationship between macro-invertebrate diversity and the environmental factors (plant productivity and soil nutrients) at smaller scales (Decaëns , 2010).

Macro-invertebrate diversity has been assessed along soil nutrient (Doblas-Miranda, et al. 2009), vegetation (Haddad et al., 2001), fire (Davies et al. 2014; Sileshi & Mafongoya, 2006), altitudinal (Rozen et al. 2013; Jones, 2000) and rainfall (Davies et al., 2013) gradients, with the majority of these studies focusing on selected taxa. However, the influence of soil nutrients and plant productivity on macro-invertebrate diversity remains poorly understood in African savannas. Also, previous studies in African savannas mainly focused on characterisation of selected better-known groups (such as Isoptera: termites, Coleoptera: beetles, earthworms and ants) and identification limited to higher taxa mainly because of lacking taxonomic capacity (Ayuke et al., 2009; Dangerfield, 1997; Warui et al., 2004).

In their wider taxonomic diversity spectrum, macro-invertebrates play an ecosystem engineering role through nutrient cycling, seed dispersal, bioturbation and ecosystem regulatory services (Decaëns, 2010; Lavelle et al. , 2006; Jones et al., 1994).

Few decades ago, African savannas experienced a land-use change from livestock ranching to wildlife conservation (Lindsey et al., 2008; Porensky et al., 2013; van der Waal et al., 2011). Livestock ranching became uneconomical due to droughts, depredation by large carnivores, pests, diseases such as foot and mouth (FMD) and poor markets access (Lindsey et al., 2008). For instance, a land-use audit done in the lowveld of Zimbabwe reported that wildlife conservation was more profitable than cattle (*Bos taurus*) ranching (Waterhouse, 1994). After abandonment of livestock farming, the cattle kraals acted as nutrient-rich patches hosting a distinct suit of plant species (Porensky et al., 2013; Veblen, 2012; Kizza et al., 2010). The improved soil nutrients and vegetation cover on abandoned kraals may have profound effects on macro-invertebrate assemblages which are highly sensitive to resource heterogeneity (Doblas-Miranda et al., 2009). However, biodiversity response of macro-invertebrates to abandoned kraals in African savannas has received less attention.

Therefore, this study aimed to test whether plant productivity and soil nutrients (as surrogates of productivity) affect macro-invertebrates assemblages in a semi-arid African savanna. Specifically, the objectives of the study were to compare between abandoned kraals and surrounding savanna plots (hereafter controls) for (1) soil nutrient properties and plant productivity variables (herbaceous biomass, aerial and basal cover), (2) belowground and aboveground macro-invertebrate assemblages (richness, abundance and ultimately diversity) and (3) to assess the relationship between aboveground and belowground macro-invertebrate species with herbaceous productivity and soil nutrients, respectively. The study hypothesised

that abandoned kraals are nutrient-rich with increased herbaceous productivity harbouring a high diversity of macro-invertebrates.

4.2 Materials and methods

4.2.1 Study area

The study was conducted in the Save Valley Conservancy, south-eastern lowveld of Zimbabwe (20° 05´ S, 32° 00´ E) and it covers an area of about 3 387 km^2. Previously, the area was used for cattle ranching until 1992 when it shifted its business to wildlife conservation (Waterhouse, 1994). The area lies in the savanna semi-arid zone with a mean daily temperature of 35°C and rainfall ranging from 300 to 500mm per annum (Lindsey et al., 2008). Gneisses and paragneisses rocks form the larger part of the geology with gently, undulating terrain and scattered kopjes. Vegetation is mainly deciduous open woodland savanna with four major woodlands types which are kopje, riverine thicket, mopane and Combretum open and scrub mopane (Waterhouse, 1994). Herbaceous community is dominated by a mixture of annual and perennial grasses such as *Setaria*, *Panicum* and *Cenchrus* species. Among its diverse wildlife species, there is the big five: elephant (*Loxodonta africana*), buffalo (*Syncerus caffer*), leopard (*Panthera pardus*), lion (*Panthera leo*), and rhinocerous (*Diceros bicornis*) and other ungulate herbivores including zebra (*Equus quagga*), giraffe (*Giraffa camelopardalis*), impala (*Aepyceros melampus*), sable antelope (*Hippotragus niger*) and hippopotamus (*Hippopotamus amphibius*).

4.2.2. Experimental design

In order to identify the location of the former cattle enclosures, we engaged a former cattle herder who worked at the conservancy during the era of cattle ranching. The exact location of the kraals abandoned 22 years ago, was confirmed using remnant features like management

roads, water troughs and fencing posts. Fifteen abandoned kraals were identified and 12 (with a standard measurement of 100m × 100m) were conveniently selected for sampling. Similar-sized control plots were marked 200 m from each sampled kraal midpoint, at the same topographical level in order to minimise the effect of topography and soil variations (van der Waal et al., 2011). All sampling was done in the wet season (November 2014 to April 2015) when vegetation is best represented (Walker, 1976) and a period of highest activity of macro-invertebrates (Anderson & Ingram, 1993).

4.2.3. Soil sampling and analyses

In each sampling plot, five samples were randomly collected using a soil auger to a depth of 15 cm and thoroughly mixed to obtain a composite sample. In order to ascertain that kraal sites are nutrient rich patches, soil samples were analysed for available phosphorus (P), mineral nitrogen (N), extractable potassium (K), exchangeable calcium (Ca), sodium (Na) and magnesium (Mg), organic carbon (C) and pH. Analyses were based on standard laboratory techniques on soil analyses (Anderson & Ingram, 1993; Motsara & Roy, 2008). Mineral N was determined by micro-Kjeldahl digestion followed by distillation, available P was measured spectrophotometrically following the Olsen's method and extractable K by a flame photometry (Motsara & Roy, 2008). Exchangeable cations (Ca, Mg and Na) were extracted with ammonium acetate and then measured using atomic absorption spectrophotometry (Anderson & Ingram, 1993). Soil pH was measured using water and $CaCl_2$ suspension and Organic C was determined volumetrically following procedures described by Motsara and Roy, (2008). All laboratory soil analyses were conducted at the Chemistry and Soil Research Institute of the Government of Zimbabwe's Ministry of Agriculture, Mechanisation and Irrigation Development.

4.2.4. Vegetation sampling

Assessment of woody vegetation structure and composition was done in the 100m x 100m plots (kraal size) following the same procedures described in Gandiwa et al., (2011). For herbaceous vegetation (grasses and forbs), in each sampling plot, nine 100m long transects (10m apart) were selected and along each transect, 11 ($1m^2$) quadrats (10m apart) were placed. All vegetation encountered was recorded and identified to species level.

Herbaceous biomass (aboveground) was determined for each sampling plot by measuring the compressed height with a disk pasture meter dropped twice in every quadrat. Biomass was then calculated using the same equation of Trollope, (1990) as follows:

$$Biomass\ (kg\ ha^{-1}) = (\sqrt{X} \times 2260) - 3019$$

Where X is the average disk height for the sampling plot.

Basal and aerial cover estimations followed the 8-point scale by Walker, (1976) and every species found within the quadrat was recorded along with the sum cover of that species (Manier & Hobbs, 2007).

4.2.5. Macro-invertebrate sampling

The belowground macro-invertebrates were sampled using monoliths method and Berlesse funnels. Ten soil monoliths (0.25 m × 0.25 m × 0.2 m) were taken randomly from each sampling plot using a steel monolith. The soil was removed and sifted carefully by hand on cardboard trays picking visible macro-invertebrates and the remaining macro-invertebrates were flushed out using Berlese funnels (Boyce, 2005).

For aboveground (including litter) macro-invertebrates, 10 pitfall traps (polyethylene containers of height 13.00 cm, diameter 5.50 cm) were randomly buried to rim level in each plot filled with soapy water to avoid escape of captured macro-invertebrates (Warui et al., 2004;

Sørensen et al., 2002). Contents were collected after 24 hours and placed in 70% alcohol prior to identification. Sweep nets (40 cm diameter) were swung randomly in each plot for a period of 2 hours. After every ten sweeps contents were emptied into glass bottles.

Sorting and identification of specimen was done morphologically classifying macro-invertebrates to the lowest taxonomic level possible (order, family, genus and species) using field guide to insects for southern Africa (Picker et al., 2004), museums' specimens, photographs and identification keys. Specimens were identified at the Bulawayo Natural History Museum and voucher specimens are housed at Bindura University of Science Education.

4.2.6. Data analyses

Data was tested for normality and homogeneity of variance and transformed as necessary. All percentage data were arcsine transformed before analysis. All univariate summary statistics were calculated in Past v.3 (Hammer, 2009) unless or otherwise stated. Analyses for belowground and aboveground macro-invertebrates were done separately. Sampling adequacy of macro-invertebrates was assessed using individual based rarefaction curves computed in Estimate S (Colwell, 2001). Comparisons of soil nutrient concentration, herbaceous productivity (biomass, aerial and basal cover) and diversity measures between abandoned kraals and control plots, were done using paired *t*-test. Diversity of macro-invertebrates was assessed using the observed species richness and abundance, evenness and diversity indices (1) Shannon-Wiener (H′) and (2) Hill number (N1). Compositional differences in macro-invertebrate assemblages and patterns in the data between abandoned kraals and control plots were explored using the analysis of similarity (ANOSIM) in R software (R Development Core Team, 2011). We used a constrained redundancy analysis (RDA) in CANOCO 4.5 (Lepš & Šmilauer, 1999) to test the relationship between aboveground and belowground macro-

invertebrates with herbaceous productivity and soil nutrients respectively. The RDA was selected because the first axis of the detrended correspondence analysis (DCA) of the data set had a gradient length less than 4 standard deviation units (Lepš & Smilauer, 2003). Infrequent taxa with abundances less than five individuals were eliminated (Riggins et al., 2009) and abundances were $\log_{10}$ transformed for a redundancy analysis (Lepš & Šmilauer, 1999). Significance of axes and explanatory variables was tested by Monte Carlo tests (999 permutations) and ordination diagrams were constructed for the first and second axes.

4.3 Results

4.3.1. Influence of abandoned kraals on soil characteristics

Concentrations of mineral N, available P, pH, extractable Ca and K were significantly higher ($P < 0.05$) on abandoned kraals than control plots (Table 4). However, no significant differences were recorded in concentrations of extractable Mg, Na and organic C between abandoned kraals and control plots ($P > 0.05$, Table 4).

Table 4. Comparisons of soil nutrients between abandoned kraals and control plots in Save Valley Conservancy, (mean ± standard error, *df* = 11).

Soil variable	Kraal	Control	*t-value*	P-value
Mineral N (ppm)	29.40 ± 2.71	17.00 ± 1.75	3.70	**0.003**
Avail. P (ppm)	42.92 ± 3.97	29.83 ±2.49	3.08	**0.010**
pH ($CaCl_2$)	5.30 ± 0.13	4.66 ± 0.20	2.96	**0.012**
Ex Ca (me%)	2.08 ± 0.15	1.58 ± 0.14	3.07	**0.011**
Ex Mg (me%)	1.15 ± 0.12	1.03 ± 0.15	0.58	0.569
Ex Na (me%)	0.24 ± 0.02	0.23 ± 0.02	0.19	0.849
Ex K (me%)	0.88 ± 0.16	0.34 ± 0.04	3.09	**0.010**

Organic C (%)	1.47 ± 0.61	1.01 ± 0.39	0.52	0.609

Significant P-values (P < 0.05) are shown in bold.

4.3.2. Influence of abandoned kraals on herbaceous productivity

Herbaceous productivity variables were significantly influenced by location. Herbaceous aerial cover, basal cover and biomass were significantly higher on kraals than controls plots (P < 0.05, Fig. 6).

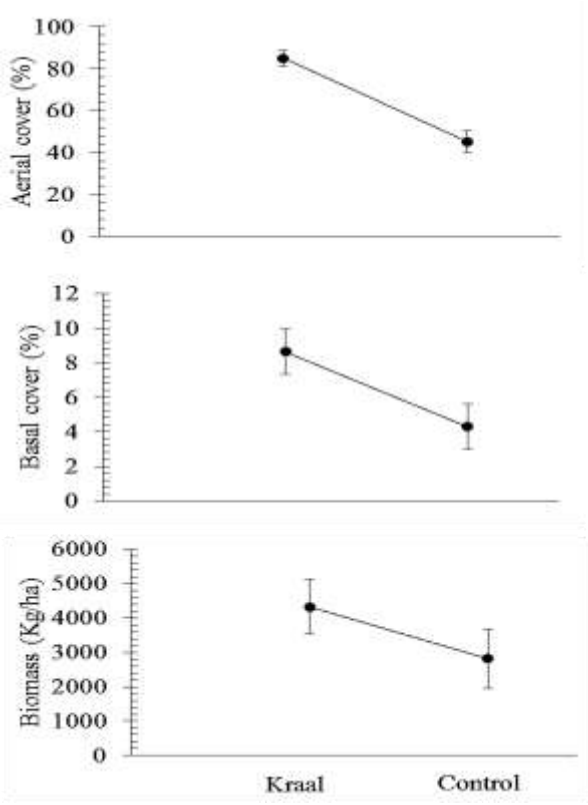

Figure 6. Comparisons of herbaceous productivity variables between abandoned kraals and control plots (mean ± standard error) in Save Valley Conservancy.

4.3.3. Soil macro-invertebrates community composition

A total of 1852 individuals were collected during the study period. Aboveground macro-invertebrates accounted for 1289 individuals with 61% found on abandoned kraals. Abandoned kraals were dominated by family Formicidae: *Pachycondyla tarsata* (25%), *Myrmicaria natalensis* (21%) and Lygaeidae: *Carbula marginella* (7%) and control plots were also

dominated by *Pachycondyla tarsata* (20%), *Myrmicaria natalensis* (12%) and Pyrrhocoridae*: Dysdercus intermedus* (12%).

Belowground macro-invertebrates had 563 individuals with 64% found on kraals. Dominant invertebrates found on kraals were Isoptera: *Macrotermes michaelseni* (22%), Tenebrionidae: *Tenebrio molitor* (23%) and Pyrrhocoridae sp. (19%). Control plots had 201 individuals dominated by *Macrotermes michaelseni* (28%), *Dysdercus intermedus* (17%) and Tenebrionidae: *Zophosis mniszechi* (11%) (see Appendix 1).

Species accumulation curves for aboveground macro-invertebrates for both the kraals and control plots had steep initial gradients, an indication of an increase in number of species caught with trapping effort (Fig. 7). However, all curves slightly level off with increase in number of individuals but did not reach an asymptote (Fig. 7). Similarly, analysis of similarity (ANOSIM) revealed no significant differences between kraals and control plots for both aboveground (Global R_{ANOSIM} = -0.019, P = 0.605) and belowground (Global R_{ANOSIM} = 0.12, P = 0.144) macro-invertebrate assemblages.

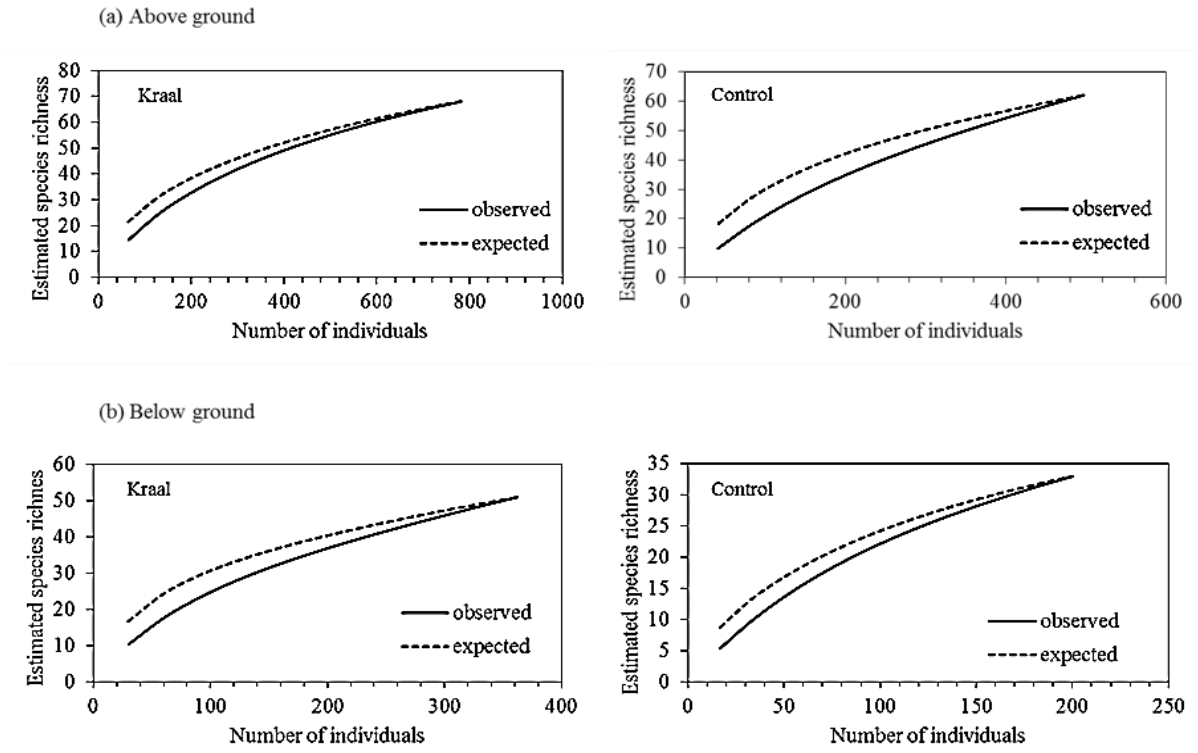

Figure 7. Individual-based species accumulation curves for aboveground (a) and belowground (b) macro-invertebrates collected from abandoned kraals and control plots in Save Valley Conservancy.

4.3.4. Influence of abandoned kraals on macro-invertebrate diversity

Species richness was significantly higher on kraals than control plots for both the aboveground and belowground macro-invertebrates ($P < 0.05$, Table 5). Abundance of belowground macro-invertebrates was significantly higher ($P < 0.05$) on kraals than controls. However, no significant difference ($P < 0.05$) in abundance was recorded between kraals and controls for aboveground macro-invertebrates although it was on average high on abandoned kraals. Diversity (Shannon-Wiener H´ and Hill N1) was significantly high ($P < 0.05$) on abandoned kraal for belowground macro-invertebrates. However, no significant differences ($P > 0.05$) in diversity were recorded for aboveground macro-invertebrates (Table 5).

Table 5. Diversity comparisons between abandoned kraals and control plots for aboveground and belowground macro-invertebrates in Save Valley Conservancy, (mean ± standard error).

		Kraal	Control	*Significance*
Aboveground	Species richness	15.83±2.59	9.92±1.74	t_{11}=4.24; **P=0.010**
	Abundance	66.92±13.96	41.42±10.64	t_{11}=1.74; P=0.110
	Evenness	0.54±0.07	0.65±0.07	t_{11}=-1.34; P=0.208
	Shannon H´	1.89±0.15	1.62±0.15	t_{11}=1.46; P=0.172
	Hill N1	7.57±1.25	5.76±0.95	t_{11}=1.54; P=0.151
Belowground	Species richness	10.33±1.20	5.42±0.67	t_{11}=4.01; P=**0.002**
	Abundance	30.17±4.10	16.75±3.05	t_{11}=3.58; P=**0.004**
	Evenness	0.70±0.03	0.76±0.07	t_{11}=-0.91; P=0.380
	Shannon H´	1.91±0.10	1.25±0.40	t_{11}=4.25; P=**0.001**
	Hill N1	7.18±0.84	3.91±0.60	t_{11}=3.36; P=**0.006**

Significant P-values (P < 0.05) are shown in bold

4.3.5 The relationship between macro- invertebrate community and environmental variables

4.3.5.1. Aboveground macro-invertebrates

Ordination RDA results, showed that the first three axes explained 26.6% of the cumulative variance of species data (Table 6). Axis1 and 2 accounted for 23.7% of the total variation. The cumulative species-environment relation of the first two axes was 89.1%. Monte-Carlo test results showed that both the first axis (F = 4.192, P = 0.001) and all axes combined (F = 2.149,

P = 0.001) explain a significantly more variation in macro-invertebrate data and the species-environment correlation for all the three axes were above 0.68. The first axis had a strong species- environment correlation (0.881) and represents a gradient of increasing herbaceous biomass (r = 0.995). Herbaceous biomass had a strong association with *Myrmicaria natalensis* and *Cletus* sp. (with the highest positive scores with axis 1) whereas the second axis represented a gradient of increasing herbaceous basal cover (r = 0.868) and highest positive scores with *Carbula marginella* and *Pachycondyla tarsata* (Fig. 8).

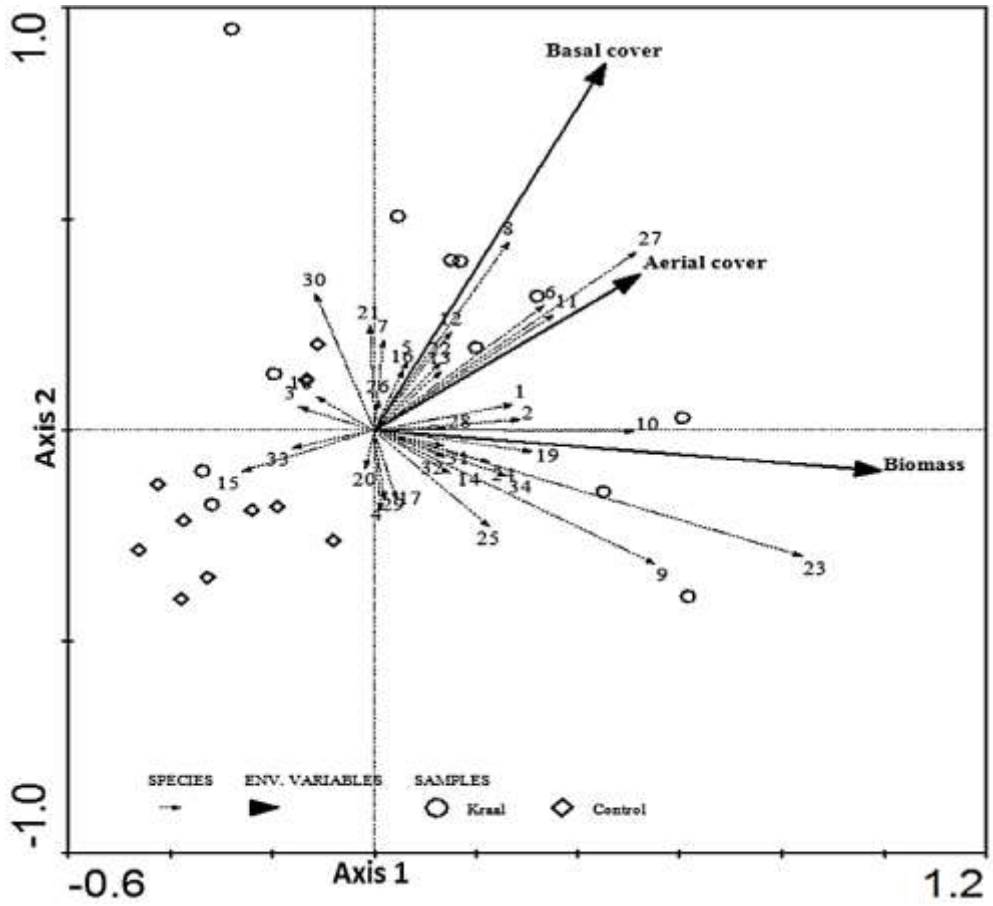

Figure 8. Ordination biplot of the redundancy analysis (RDA) for the aboveground macro-invertebrate morphospecies and environmental variables (plant) from abandoned kraals and control plots in Save Valley Conservancy. 1:*Acraea* sp.; 2: *Acrididae* juvenile.; 3:*Adesmia schouteni*; 4: *Altractonotus mulsanti*; 5: *Anachalcos convexus*; 6: *Aspilocoryphus fasciativentris*; 7: *Belenois aurota*; 8: *Carbula marginella*; 9: *Catacops melanostica*; 10: *Cletus* sp.; 11: *Copris elpharon*; 12: *Cubionidae* sp.; 13: *Dieuches armipes*; 14: *Dysdercus intermedius*; 15: *Geocnethus plagiata*; 16: *Gnaphosidae* larvae; 17: *Lepidoptera* larvae; 18: *Ligariella* sp.; 19: *Lycosidae* juvenile.; 20: *Messor capensis*; 21: *Morphacris fasciata*; 22: *Mylabris pollita*; 23: *Myrmicaria natalensis*; 24: *Oedaleus* sp.; 25: *Oncopeltus famelicus*; 26: *Oxycarenus hyalipennis*; 27: *Pachycondyla tarsata*; 28: *Phaneratoma arnoldii*; 29:

Piezomastax sp.; 30: *Plagiodera caffra*; 31: *Ruspolia differens*; 32: *Scantius forsteri*; 33: *Tenebrio molitor* and 34: *Zophosis mniszechi*

Table 6. Ordination RDA results for above and belowground soil invertebrates and environmental variables for the first three and four axes respectively showing the relationship between the macro-invertebrate community and the environmental variables on abandoned kraals and control plots in Save Valley Conservancy.

	Axis 1	Axis 2	Axis 3	Axis 4
Aboveground macro-invertebrates				
Eigenvalues	0.173	0.064	0.029	
Species-environment correlations	0.881	0.700	0.684	
Cumulative % variance of species data	17.3	23.7	26.6	
Cumulative % variance of species-environment relation	65.1	89.1	100	
Intraset correlation coefficients				
Basal cover	0.454	0.868	0.202	
Biomass	0.995	-0.097	0.026	
Aerial cover	0.521	0.368	-0.770	
Belowground macro-invertebrates				
Eigenvalues	0.063	0.051	0.032	0.028
Species-environment correlations	0.8	0.683	0.663	0.523
Cumulative % variance of species data	6.3	11.5	14.7	17.5
Cumulative % variance of species-environment relation	34.4	62.2	79.7	94.9
Intraset correlation coefficients				
Mineral N	0.320	0.054	0.796	-0.481
Available P	0.746	0.149	0.140	0.470
pH	0.246	-0.040	0.510	0.235
Extractable K	0.050	0.694	0.678	0.148
Organic C	0.578	0.433	-0.503	-0.301

4.3.5.2. Belowground macro-invertebrates

The RDA for belowground invertebrates explained 17.5% of the total variation in species data (Table 6). The first three axes accounted for 14.7% of the cumulative variance of species data (Table 3). The cumulative species-environment relation of the first three axes was 79.7%. Monte-Carlo test results showed that both the first axis (F = 1.13, P = 0.913) and all axes combined (F = 0.81 P = 0.833) explain much of the variation in belowground macro-

invertebrate data although not statistically different. All the axes had species-environment correlations greater than 0.50. The first axis had a strong species- environment correlation (0.80) and represents a gradient of increasing available P (r = 0.746) and organic C (r = 0.578). Available P and organic C had an association with *Pachylister caffer* and *Scolopendra morsitans* (with the highest positive scores with axis 1). The second axis seem to represent a gradient of increasing extractable K (r = 0.694) and highest positive scores with *Blaberidae* sp. whereas the third axis represent mineral N (r = 0.796) and pH (r = 0.51) and have an association with *Schizonycha valida* and *Hodotermes mossambicus*. *Zophosis mniszechi* and *Scantius forsteri* had the highest negative scores associated with axes 1and 3 (Fig. 9).

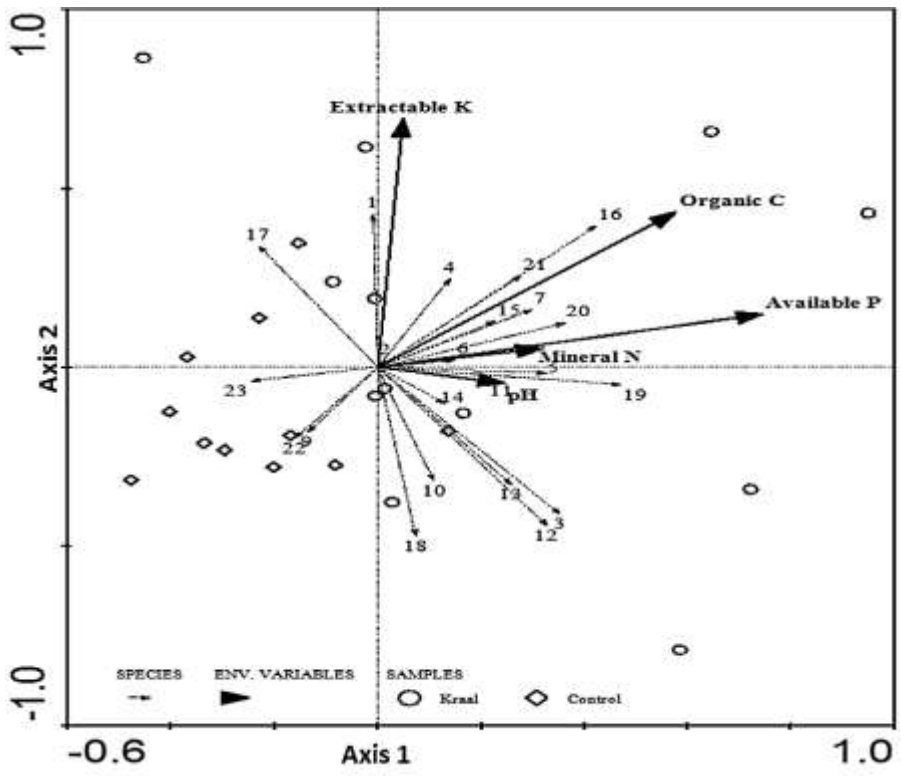

Figure 9. Ordination biplot of the redundancy analysis (RDA) for the belowground macro-invertebrate morphospecies and environmental variables (soil) from abandoned kraals and control plots in Save Valley Conservancy. 1:*Blaberidae* sp.; 2: *Blattidae* larvae; 3:*Camponotus maculatus;* 4: *Carabidae* larvae.; 5: *Carbula marginella*; 6: *Cormocephalus* sp.; 7: *Dysdercus intermedius*; 8: *Formicidae* larvae; 9: *Geocnethus plagiata*; 10: *Gnaphosidae* larvae.; 11: *Hodotermes mossambicus*; 12: *Lepidoptera* larvae; 13: *Lycosidae* larvae; 14: *Macrotermes michaelseni*; 15: *Pachycondyla tarsata*; 16: *Pachylister caffer*; 17: *Parena ferruginea*; 18: *Scantius forsteri*; 19: *Schizonycha valida;* 20: *Scolopendra morsitans*; 21: *Tenebrio molitor*; 22: *Tetraponera* sp.; 23: *Zophosis mniszech*

4.4 Discussion

Our study provides some novel insights regarding the influence of soil nutrients and herbaceous productivity on macro-invertebrates richness and diversity in a semi-arid African savanna ecosystem. Higher levels of soil nutrients and herbaceous productivity recorded on abandoned kraals were in line with our hypothesis. Macro-invertebrate species responded positively to an increase in soil nutrient and herbaceous productivity which indicates that former kraals are strong forces to savanna spatial heterogeneity, with implications on biodiversity and ecosystem functioning.

4.4.1. Influence of abandoned kraals on soil and vegetation characteristics

We recorded higher levels of soil nutrients on abandoned kraals than control (savanna) plots as in other studies (Kizza et al., 2010; Muchiru et al., 2009; Porensky et al., 2013; van der Waal et al., 2011). Soil nutrients have been demonstrated to persist in the soil for decades after abandonment of kraals, being maintained primarily by plant-soil-herbivore nutrient feedback loop (Augustine & McNaughton, 2006; van der Waal et al., 2011). Large herbivores are often attracted to nutritious forage growing on abandoned kraals and possibly drop dung and urine during feeding, which persistently enrich these sites. The cascading effects of soil nutrients at these sites, stimulates both soil macro and micro-invertebrates (Bardgett & Wardle, 2003) thereby accelerating nutrient mineralisation. For example soil nitrogen was 1.7 times higher on abandoned kraals than control plots probably because of a sustained organic matter mineralisation. Phosphorus was significantly higher (1.4 times) on abandoned kraals than control plots owing to mineral complexes it forms in soil that minimises leaching and external sourcing by herbivores (Porensky et al., 2013). Soil pH was slightly acidic on both sites although control plots were more acidic than abandoned kraals probably due to the acidic leaf litter from woody species (Sayad et al., 2012). These soil results corroborates results of Veblen

(2012), who has recorded high levels of nitrogen and phosphorus (3.8 and 6.8 times respectively) on abandoned kraals and an increase in base cations (Ca and Mg) on Kenyan savanna plots and further suggested the influence of site age and nutrient accumulation.

Herbaceous productivity (biomass, basal and aerial cover) was significantly higher on abandoned kraals than control plots showing the response of plants to elevated limiting soil nutrients. Other studies have demonstrated similar results that abandoned kraals harbour a higher herbaceous productivity compared to the surrounding matrix (Young et al. 2013; van der Waal et al., 2011; Veblen & Young, 2010; Muchiru et al., 2009). Higher herbaceous productivity on abandoned kraals could also be attributed to the dominance of forbs with thick culms and branches which could easily suspend the disk pasture meter off the ground giving inflated values for biomass estimation.

4.4.2. Influence of kraal sites on macro-invertebrate assemblages.

Regardless of site, savanna matrix or abandoned kraals, the observed high abundances of species belonging to orders Hymenoptera, Hemiptera, Coleoptera and Isoptera recorded in the present study, are comparable to other studies (Ayuke et al., 2009; Muchane et al., 2012). Specifically, dominant families on abandoned kraals were Formicidae (ants), Scarabaeidae and Tenebrionidae (beetles), Lygaeidae (bugs) and Termitidae (termites) which were also recorded as the dominant macro-invertebrates on nutrient-rich habitats elsewhere (Doblas-Miranda et al., 2009; Marchão et al., 2009). Presence of Isopterans and Coleopterans in high abundances can be explained by the effect of our sampling period which coincided with their period of highest activity.

Species richness was significantly higher on abandoned kraals for both below and aboveground habitats, an indication that abandoned kraals are a favourable habitat in terms

feed quality and quantity that supports a variety of macro-invertebrates (Wardle et al., 2004). Other studies also recorded a high species richness of soil macro-invertebrates on nutrient-rich habitats (Manyanga et al., 2014; Doblas-Miranda ,et al. 2009; Ayuke et al., 2009; Hemerik & Brussaard, 2002). Unlike belowground invertebrates, species abundance for the aboveground habitat was not significantly different in both sites pointing to the ability of most species to traverse long distances during foraging thereby exhibiting an even distribution. In this study, a 100m distance between kraals and control plots could have been traversed during foraging and dispersal. For example, Formicides and Isopterans forage over long distances from their nests and practice swarming when new reproductives fly to establish new colonies (Doblas-Miranda et al., 2009). Furthermore, Shannon Wiener diversity did not vary for aboveground species. This is contrary to our hypothesis that diversity would be high on abandoned kraals because of its high levels of plant and litter biomass. Also, this result is not in line with productivity-diversity hypothesis (Grime, 1973) and other empirical studies (Mathieu et al., 2009; Doblas-Miranda et al., 2009; Laossi et al., 2008, Siemann, 1998) where macro-invertebrate diversity significantly increased with an increase in plant productivity. This can be accounted for by the generalist feeding behaviour and habitat preference (relatively unresponsive to small changes in resource quality) by aboveground invertebrates (Laossi et al., 2008). On the other hand, improved plant productivity and habitat conditions on abandoned kraals might have facilitated competitive exclusion leading to the dominance of a few species (Grime, 1973), thereby maintaining a similar diversity with the control plots.

Considering the RDA results for aboveground macro-invertebrates (Fig. 8) phytophagous *Carbula marginella*, *Cletus* sp. and predacious ants *Pachycondyla tarsata* and *Mymicaria natalensis* had an association with plant variables. Phytophagous hemipterans could have been attracted by vigorous plants especially the dominant forb species found on

abandoned kraals (Veblen, 2012) whereas predacious ants favour prey-rich areas like beneath grasses (López et al., 2000). RDA results for belowground macro-invertebrates (Fig. 9) indicated that the Myriapods (*Scolopendra morsitans*), Coleopterans *(Pachlister caffer*), and Isopterans (*Hodotermes mossambicus*) benefited most from high concentration of limiting soil nutrients (N, P, K and C) on abandoned kraals. Similar findings have been recorded on nutrient-rich areas by others (Doblas-Miranda et al., 2009; Riggins et al., 2009; Wu et al., 2015; Salamon et al., 2011). Soils rich in N, P, K and C are associated with high microbial biomass (Lavelle, 1997) which could have directly or indirectly attracted these species. Dung and carrion which is commonly found on abandoned kraals (Riginos et al., 2012) could have attracted a wide variety of coprophagous and necrophagous species for instance the Coleopterans (Salamon et al., 2011). On the other hand, abandoned kraals enhance the micro-climate for a variety of soil and litter dwellers (Fig. 9) through good nutrient supply for plant growth (Muchiru et al., 2009) and ultimately improved quality and quantity of litter (Mathieu et al., 2009).

4.5 Conclusions

Our study shows that abandoned kraals as long-term nutrient-rich habitat patches, have a significant influence on abundance and richness of macro-invertebrates. In line with our hypothesis, abandoned kraals were still soil nutrient-rich and had a significantly high richness and abundance of belowground macro-invertebrates. However, the diversity of aboveground macro-invertebrates did not respond to the influence of abandoned kraals. Soil nutrient properties and herbaceous productivity had a positive influence on relative abundances on some belowground and aboveground macro-invertebrate taxa as shown by significant correlations. Therefore, results suggest that nutrient heterogeneity due to abandoned kraals affect the belowground macro-invertebrates more than the highly mobile aboveground taxa.

However, in order to fully ascertain the influence of habitat productivity on macro-invertebrate assemblages, further research is needed on the horizontal mobility of each taxon and its sensitivity to resource heterogeneity at both spatial and temporal scales on nutrient hotspots in a semi-arid savanna.

4.6 Acknowledgements

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Appendix 1: Checklist of macro-invertebrates (above and belowground) found on abandoned kraals and control plots in Save Valley Conservancy, Zimbabwe.

			Total	
Order	Family	Genus/ species	Kraals	Controls
Amblypygi	*Amblypygidae*	*Damon* sp.	2	-
Acarina	*?*	*	-	1
Araneae	*Araneidae*	*	2	-
	Corrinnidae	*	4	-
	Cubionidae	*	8	-
	Gnaphosidae	*	8	7
	Heteropodidae	*	-	1
	Lycosidae	*	19	4
	Salticidae	*	3	-
	Selenopidae	*Selenopes sp.*	2	-
	Thomisidae	*	1	2
	Zodarridae	*	1	1
Blattodea	*Blaberidae*	*Hostilia sp.*	13	5
	Blattidae	juvenile	5	-
Coleoptera	*Carabidae*	larva	15	2
		Cypholoba alveolata	1	-
		Anthia pachyoma	2	-
		Altractonotus mulsanti	2	5
		Poecilothais tetragramma	1	-
		Dromica spectabilis	-	2
		Parena ferruginea	2	7
	Chysomelidae	*Plagiodera caffra*	3	6
		Crabonites equestris	1	2
	Coccinellidae	*Cheilomenes lunata*	2	-
		Henosepilachna bifasciata	1	-
	Curculionidae	*Calodemas nickerli*	-	2
	Histeridae	*Pachylister caffer*	8	-
	Meloidae	*Mylabris pollita*	3	2
	Scarabaeidae	*Anachalcos convexus*	8	12
		Aphodius spp.	1	1
		Copris elpharon	19	2
		larva	1	1
		Kheper nigroaeneus	-	1
		Onitis fulgidus	1	-
		Onitis westermanni	2	-
		Schizonycha valida	11	2
	Tenebrionidae	*Adesmia schouteni*	31	22
		Anomalipus polymorphus	-	2

		Endustomus parallelogrammus	1	-
		Eurychora sp.	4	-
		Phanerotoma arnoldi	4	6
		Phanerotoma scobicolle	-	1
		Psammodes virago	4	-
		Stips dohrni	1	-
		Tenebrio molitor	50	7
		Zophosis mniszechi	31	32
	Trogidae	*Trox sulcatus*	1	-
Diptera	Asilidae	*Philodicus* sp.	2	-
Hemiptera	Coreidae	*Cletus sp.*	17	2
		Oxycarenus hyalipennis	16	1
		Pephricus sp.	1	1
	Cydnidae	*Geocnethus plagiata*	8	8
	Lygaeidae	*Aspilocoryphus fasciativentris*	41	5
		Carbula marginella	60	5
		Dieuches armipes	1	6
		Graptostethus servus	1	-
		*	3	2
		Oncopeltus famelicus	25	22
	Pentatomidae	*Nezara virudia*	1	1
		*	5	-
		Diploxys fallax	-	1
	Pyrrhocoridae	*Dysdercus intermedus*	71	97
		Scantius forsteri	28	11
	Reduviidae	*Leptodena acanthoocephalum*	1	-
Homoptera	Eurybrachidae	*Aselgela ramulifera*	3	-
Hymenoptera	Formicidae	*Camponotus maculatus*	17	5
		Messor capensis	7	25
		Myrmicaria natalensis	161	68
		Pachycondyla tarsata	275	75
		*	6	-
		Polyrhachis sp.	-	1
		Tetraponera sp.	4	4
	Mutillidae	*Mutilla astarte*	2	-
	Ichneumonidae	*Archibracon serviellei*	1	-
Isoptera	Hodotermitidae	*Hodotermes mossambicus*	19	8
	Termitidae	*Macrotermes michaelseni*	26	71
Lepidoptera	Nymphalidae	*Acraea* sp.	16	7
		Charaxes sp.	2	2
	Pieridae	*Belenois aurota*	2	7

	?	larva	20	7
Mantodea	Mantidae	juvenile	2	-
		Ligariella sp.	3	2
		*	2	1
		Tarachodes	-	1
	Thespidae	*Hoplocoryphella grandis*	1	-
Myriapoda	Odontopygidae	*	4	-
	Scolopendromopha	*Cormocephalus* sp.	5	6
		Scolopendra morsitans	8	2
Neuroptera	Myrmeleontidae	*Palpares* sp. (larva)	2	1
Orthoptera	Acrididae	*Acrida acuminata*	4	-
		Catacops melanostica	5	5
		Humbe tenuicornis	3	-
		larva	1	3
		Morphacris fasciata	15	2
		Oedaleus sp.	6	9
		*	1	-
		Orthoctha sp.	-	4
		Piezomastax sp.	21	6
	Gryllidae	*juvenile*	6	2
		*	1	-
	Lentulidae	*Mecostibia mopane*	1	-
	Pamphagidae	*Lamarkiana puntosa*	-	1
		*	3	-
	Tettigoniidae	*Russipolia differens*	7	1
Scorpiones	Scorpionidae	*Opistophthalmus glabrifrons*	2	-
	Buthidae	*Parabothus transvaalicus*	-	1
Solpugida	Solfugidae	*	-	1

Symbols: ? = unknown family, * = unknown genus/ species

CHAPTER 5

Functional diversity of macro-invertebrates on abandoned cattle enclosures in a semi-arid African savanna*

* *This Chapter was published as:*

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Abstract

Zimbabwe is experiencing a shift in land-use, away from livestock farming and towards wildlife conservation. The abandonment of livestock farming may have unforeseen consequences on biodiversity and ecosystem functioning, as cattle kraals create valuable nutrient-rich patches across the semi-arid savannah. It is unclear how macroinvertebrates functionally respond to such nutrient-rich patches in semiarid savannahs. We analysed functional diversity of both aboveground and belowground taxa on abandoned cattle kraals and savannah control plots in Save Valley Conservancy (SVC). We used distance-based multivariate techniques to estimate indices of functional diversity. Our results indicated that after two decades of abandonment, kraals had higher functional richness (FRic), functional divergence (FDiv) and functional dispersion (FDis) of macroinvertebrates when both aboveground and belowground species are combined. When aboveground macroinvertebrates were considered alone, no difference was observed for all the considered functional indices. However, only FRic was higher on kraals when belowground macroinvertebrates were separately considered. Our results suggest that two-decade-old abandoned kraals may have recovered enough for aboveground species to match the surrounding savannah plot and even surpassed the savannah control for belowground species functional diversity.

Keywords: functional diversity, macro-invertebrates, abandoned kraals, nutrient-hotspot

5.1 Introduction

Understanding the implications of ecosystem heterogeneity on biodiversity and ecosystem functioning is a fundamental goal in ecology. At a finer scale, the periodic creation and abandonment of livestock areas in the sub-tropical savannas, have an influence on the stability and resilience of ecosystems (Muchiru et al., 2009; Riginos et al., 2012; Veblen, 2012). For instance, varying levels of productivity on disturbed habitats may alter the diversity of species and their functional roles through disturbance (Huston, 2014) and competition (Grime, 1973).

Abandoned kraals have been studied as nutrient-rich patches compared to the surrounding matrix with a potential to influence ecosystem services (Decaëns et al., 2004; Muchiru et al., 2009; Porensky et al., 2013; Veblen & Young, 2010). For example, abandoned kraals influence herbivory (Augustine & McNaughton, 2006), plant and nutrient succession (Decaëns et al., 2004; Muchiru et al., 2009) and vegetation structure and composition (van der Waal et al., 2011; Young et al., 2013). Similarly, soil nutrient enriched sites can affect the quality and quantity of feed resources which is a key factor for the establishment of macro-invertebrate species (Decaëns et al., 2004). Moreover, soil macro-invertebrates are sensitive to nutrient concentrations for instance, maintains a strict internal and external chemical balance (Mathieu et al., 2009), any small changes to habitat resources may alter their assemblage structure and ecological function.

As ecosystem engineers (Jones et al., 1994), soil macro-invertebrates play a significant role in the decomposition of organic matter through fragmentation and comminution of litter and provision of substrate and dispersal of microbial propagules (Cole et al., 2006; Decaëns, 2010). In nutrient cycling, macro-invertebrates facilitate nitrogen mineralisation and fixation (Lavelle et al., 2006). Further, the movement of belowground macro-invertebrates improves soil structure through bioturbation and play a pivotal role in ecosystem regulatory services

(Decaëns, 2010). Therefore, abandoned cattle enclosures with elevated soil properties (Kizza et al., 2010) and vigorous plants (van der Waal et al., 2011) enriched with herbivores' dung and urine might have a profound effect on macro-invertebrate functional assemblages. Although several studies investigated the influence of abandoned kraals on soil nutrient dynamics (Kizza et al., 2010), vegetation development (Porensky et al., 2013; Veblen & Young, 2010) forage quality and herbivory (Augustine & McNaughton, 2006; van der Waal et al., 2011), their effect on functional response of macro-invertebrates is less studied.

There is growing attention on the use of functional diversity to predict ecosystem functioning after a disturbance (Petchey et al., 2004). However, a considerable research effort is focused on aquatic invertebrates (Bremner et al., 2003; Cummins et al., 2005) and plants (Joseph et al., 2014; Roscher et al., 2012; Symstad et al., 2000). Functional response of terrestrial macro-invertebrates to disturbance is still lagging in knowledge. As noted by Hemerik and Brussaard, (2002), this might be primarily due to a poor recognition of functional roles of soil macro-invertebrates and taxonomical difficulties in identifying the highly diverse macro-invertebrates. The use of functional diversity as a measure of biotic changes to anthropogenic disturbances has recently gathered momentum. Functional diversity is the variety of functional identities of organisms in a community based on easily recognised behavioural and morphological characteristics which are directly linked to an organism's ecological performance (Mumme et al., 2015; Petchey & Gaston, 2006). Therefore, ecosystem functional stability and resilience can be easily predicted after a disturbance. Functional diversity categorise relative abundances of species with similar ecological functions into functional groups. However, due to a weak explanatory power of functional group richness in explaining the functional diversity response to disturbance (Petchey & Gaston, 2006), it can best be used nested with finer functional traits (e.g. trophic group analyses) supported by appropriate

multivariate distance-based metric functional dispersion statistical analyses (Mumme et al., 2015; Petchey et al., 2004).

Earlier studies in the semi-arid sub-tropical savannas documented the functional response of macro-invertebrates in agro-ecosystems (Ayuke et al., 2009; Giller et al., 1997; Manyanga et al., 2014). To our knowledge no study has investigated the impact of abandoned kraals on functional diversity of macro-invertebrates. In this study we aimed to assess the diversity of functional trait response of macro-invertebrates to relatively small nutrient patches (kraals) contrasted with the surrounding savanna habitat matrix. Given that soil macro-invertebrates are influenced by soil properties (Doblas-Miranda et al., 2009), and vegetation structure and composition (Haddad et al., 2001; Mumme et al., 2015), and that abandoned kraals harbour elevated soil nutrients and quality forage (Riginos et al., 2012; van der Waal et al., 2011), our functional group responses were based on soil and vegetation properties. We predicted that (1) the nutrient-rich abandoned kraals would have higher functional diversity response of macro-invertebrates than the surrounding savanna habitat (hereafter control plots) (2) functional diversity of aboveground and belowground macro-invertebrates would respond differently on kraals and controls (3) functional group richness would be higher on kraals than controls.

5.2 Methods

5.2.1 Study system

The study was conducted in the Save Valley Conservancy (3387 $km^{2)}$ located in south-eastern Lowveld of Zimbabwe (20°05´S, 32°00´E). Previously, the area was a cattle ranching site (Devuli ranch) until 1992 when it shifted its business to wildlife conservation (Waterhouse, 1994). The area lies in semi-arid zone with a mean daily temperature of 35°C and rainfall ranging from 300-500mm per annum (Lindsey et al., 2008). The geology consists largely of

gneisses and paragneisses forming gently, undulating terrain with scattered (Lindsey et al., 2008). Vegetation is mainly deciduous open woodland savanna with four major woodlands types which are kopje, riverine thicket, Mopane and Combretum open and scrub mopane (Waterhouse, 1994). Herbaceous community is dominated by a mixture of annual and perennial grasses such as *Setaria*, *Panicum* and *Cenchrus* species. The commonly found macro-invertebrates include Isopterans, Formicids, Lygaeds and Pyrrhocorids. Among its diverse wildlife species, there is the big five and other ungulate herbivores including zebra (*Equus burchelli*), giraffe (*Giraffa camelopardalis*), impala (*Aepyceros melampus*), sable antelope (*Hippotragus niger*) and hippopotamus (*Hippopotamus amphibius*).

5.2.2 Sampling design

Data on macro-invertebrate communities, soil and vegetation properties were collected in twelve abandoned kraals ($100m^2$) paired with similar-sized control plots from the adjacent savanna matrix. Control plot midpoints were marked 200m from abandoned kraals' midpoints at the same topographical level to minimise soil and environmental variability following van der Waal et al., (2011). Sampling was done from November 2014 to April 2015 (rainy season).

5.2.3 Soil sampling and analyses

In each sampling plot, five samples were randomly collected using a soil auger to a depth of 15 cm and thoroughly mixed to obtain a composite sample. In order to ascertain that kraal sites are nutrient rich patches, soil samples were analysed for available phosphorus (P), mineral nitrogen (N), extractable poattasium (K), exchangeable calcium (Ca), sodium (Na) and magnesium (Mg), organic carbon (C) and pH. Analysis of the soil properties was based on standard laboratory techniques on soil analyses (Anderson & Ingram, 1993; Motsara & Roy, 2008). Mineral N was determined by micro-Kjeldahl digestion followed by distillation,

available P was measured spectrophotometrically following the Olsen's method and extractable K by a flame photometry (Motsara & Roy, 2008). Exchangeable cations (Ca, Mg and Na) were extracted with ammonium acetate and then measured using atomic absorption spectrophotometry (Anderson & Ingram, 1993). Soil pH was measured using water and $CaCl_2$ suspension and Organic C was determined volumetrically following procedures described by Motsara and Roy (2008). All laboratory soil analyses were conducted at the Chemistry and Soil Research Institute of the Government of Zimbabwe's Ministry of Agriculture.

5.2.4 Vegetation sampling

Assessment of woody vegetation structure and composition was done in the 100m x 100m plots (kraal size) following the same procedures described in Gandiwa et al., (2011). For herbaceous vegetation (grasses and forbs), in each sampling plot, nine 100m long transects (10m apart) were selected and along each transect, 11 ($1m^2$) quadrats (10m apart) were placed. All vegetation encountered was recorded and identified to species level.

Herbaceous biomass (aboveground) was determined for each sampling plot by measuring the compressed height with a disk pasture meter dropped twice in every quadrat. Biomass was then calculated using the same equation of Trollope, (1990) as follows:

$$Biomass\ (kg\ ha^{-1}) = (\sqrt{X} \times 2260) - 3019$$

Where X is the average disk height for the sampling plot.

Basal and aerial cover estimations followed the 8-point scale by Walker (1976) and every species found within the quadrat was recorded along with the sum cover of that species (Manier & Hobbs, 2007).

5.2.5 Macro-invertebrate sampling

The belowground macro-invertebrates were sampled using monoliths method and Berlesse funnels. Ten soil monoliths (0.25 m × 0.25 m × 0.2 m) were taken randomly from each sampling plot using a steel monolith. The soil was removed and sifted carefully by hand on cardboard trays picking visible macro-invertebrates and the remaining macro-invertebrates were flushed out using Berlese funnels (Boyce, 2005).

For aboveground (including litter) macro-invertebrates, 10 pitfall traps (polyethylene containers of height 13.00 cm, diameter 5.50 cm) were randomly buried to rim level in each plot filled with soapy water to avoid escape of captured macro-invertebrates (Warui et al. 2004; Sørensen et al. 2002). Contents were collected after 24 hours and placed in 70% alcohol prior identification. Sweep nets (40 cm diameter) were swung randomly in each plot for a period of 2 hours. After every ten sweeps contents were emptied into glass bottles.

Sorting and identification of specimen was done morphologically classifying macro-invertebrates to the lowest taxonomic level possible (order, family, genus and species) using field guide to insects for southern Africa (Picker et al., 2004), museums' specimens, photographs and identification keys. Specimens were identified at the Bulawayo Natural History Museum and voucher specimens are housed at Bindura University of Science Education.

5.2.6 Trait selections

We classified every morphospecies into five different ecological traits: feeding group (predacious, saprophagous, omnivorous, parasitic and phytophagous), ecosystem engineering (soil organic matter transformation and nutrient cycling, litter transformers and bioturbation), eusociality (eusocial or non-eusocial), dispersal capacity (wings, legs or both) and habitat

specificity (abandoned kraals, savanna matrix or both). We followed trait selection protocols described in Mumme et al. , (2015) and Audino et al., (2014). Additional trait information was obtained from literature and entomological specialists.

5.2.7 Data analyses

For parametric tests, data were first tested for normality and all non-normal, percentage and concentration data were transformed as necessary to improve data distribution. Analyses separated belowground (monoliths and Berleese funnels) and aboveground macro-invertebrates (pitfalls and sweepnets) (Doblas-Miranda, et al. 2009; Hemerik & Brussaard, 2002). A paired *t*-test was used to test whether abandoned kraals have a higher level of soil nutrients and herbaceous variables than the control plots. Sampling adequacy for aboveground and belowground habitats was assessed using individual-based species accumulation curves (Coleman rarefaction) computed in Estimate S (Colwell, 2013). Patterns in the data (compositional differences) were explored using analysis of similarity (ANOSIM) in R software (R Development Core Team, 2011).

5.2.7.1 Functional diversity

Using the five selected traits, we first divided the morphospecies into functional response groups using the 'FD' package in R software (R Development Core Team, 2011). Then we computed a Gower dissimilarity (gowdis) and constructed a species trait-based dendrogram and selected functional groups based on their trait combinations (Laliberte & Legendre, 2010; Mumme et al., 2015). Care was taken not to choose functionally dissimilar species.

We assessed functional diversity for aboveground and belowground habitat compartments (Doblas-Miranda, 2009) and between abandoned kraals and savanna habitat. We calculated

functional diversity indices: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) (Villéger, 2008) and functional dispersion (FDis) (Laliberte & Legendre, 2010) using the dbFD function in the 'FD' package for R (R Development Core Team, 2011). Functional richness is a functional space occupied by the available species in a community (Audino et al., 2014; Mouchet et al., 2010). Functional evenness represents the distribution of species relative abundances in a functional space (Audino et al., 2014). Functional divergence measures the degree to which abundance distribution in niche space maximises divergence in functional characters within the community (Villéger, 2008). Functional dispersion calculates the mean distance of species to the community trait-mean centroid weighted by their relative abundances (Laliberte & Legendre, 2010).

We compared the functional diversity indices between abandoned kraals and savanna plots using a paired *t*-test in R software (R Development Core Team, 2011). We further tested for the differences in functional response groups (FRG) between abandoned kraals and control plots using the general linear model (GLM) with a negative binomial error.

5.3 Results

5.3.1 Plant and soil data

We recorded a significantly higher ($P<0.05$) concentration of mineral N, available P, pH, extractable Ca and K on abandoned kraals than control plots. Concentrations of extractable Mg, Na and organic C were on average higher in abandoned kraals than the control plots although not statistically different at $P>0.05$ (Table 7).

Table 7. Comparisons of soil and plant variables between abandoned kraals and control plots in Save Valley Conservancy, Zimbabwe (mean ± standard error).

Variable	Kraal	Control	*t-value*	P-value
Soil characteristics				
Mineral N (ppm)	29.40 ± 2.71	17.00 ± 1.75	3.70	**0.003**
Avail. P (ppm)	42.92 ± 3.97	29.83 ±2.49	3.08	**0.010**
pH ($CaCl_2$)	5.30 ± 0.13	4.66 ± 0.20	2.96	**0.012**
Ex Ca (me%)	2.08 ± 0.15	1.58 ± 0.14	3.07	**0.011**
Ex Mg (me%)	1.15 ± 0.12	1.03 ± 0.15	0.58	0.569
Ex Na (me%)	0.24 ± 0.02	0.23 ± 0.02	0.19	0.849
Ex K (me%)	0.88 ± 0.16	0.34 ± 0.04	3.09	**0.010**
Organic C (%)	1.47 ± 0.61	1.01 ± 0.39	0.52	0.609
Herbaceous productivity				
Basal cover (%)	8.64 ± 1.31	4.31 ± 1.31	2.31	**0.04**
Aerial cover (%)	85.85 ± 3.85	45.25 ± 5.05	7.06	**<0.001**
Biomass ($kgha^{-1)}$	4321 ± 804.84	2823 ± 860.80	2.32	**0.04**

Plant productivity variables were significantly influenced by abandoned kraals. Herbaceous aerial cover, basal cover and biomass were significantly higher on kraals ($P<0.05$) than control plots (Fig. 10).

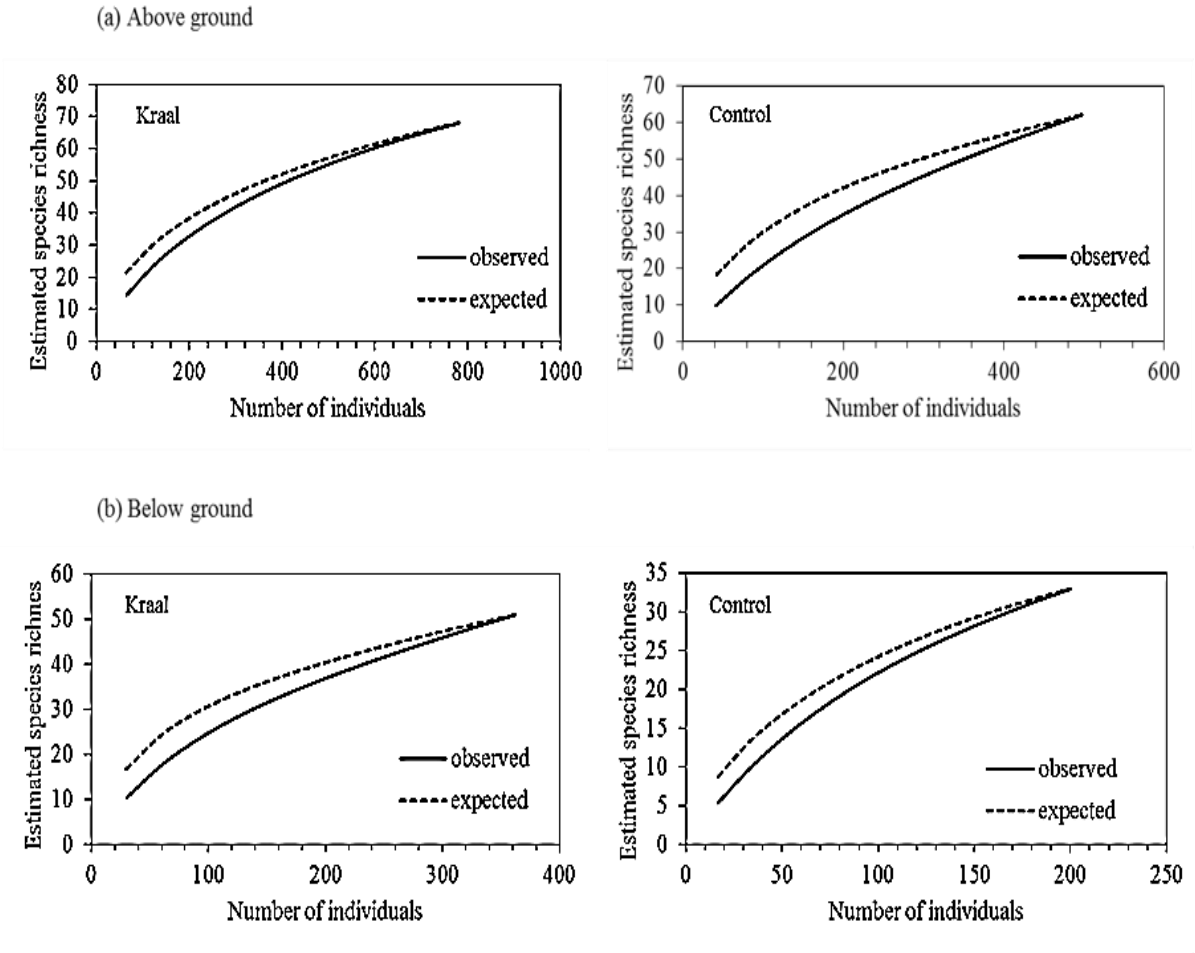

Figure 10. Individual-based species accumulation curves for (a) aboveground and (b) belowground macro-invertebrates collected from abandoned kraals and control plots in Save Valley Conservancy, Zimbabwe.

5.3.2 Macro-invertebrate community composition

A total of 1852 individuals were collected during the study period. Aboveground macro-invertebrates accounted for 1289 individuals with 61% found on abandoned kraals. Abandoned kraals were dominated by family Formicidae: *Pachycondyla tarsata* (25%), *Myrmicaria natalensis* (21%) and Lygaeidae: *Carbula marginella* (7%) and control plots were also dominated by *Pachycondyla tarsata* (20%), *Myrmicaria natalensis* (12%) and Pyrrhocoridae*: Dysdercus intermedus* (12%).

Belowground macro-invertebrates had 563 individuals with 64% found on kraals. Dominant invertebrates found on kraals were Isoptera: *Macrotermes michaelseni* (22%), Tenebrionidae: *Tenebrio molitor* (23%) and Pyrrhocoridae sp. (19%). Control plots had 201 individuals dominated by *Macrotermes michaelseni* (28%), *Dysdercus intermedus* (17%) and Tenebrionidae: *Zophosis mniszechi* (11%) (Appendix 1).

Species accumulation curves for aboveground macro-invertebrates showed that both the curves for abandoned kraals and control plots indicated steep initial gradients, an indication of an increase in number of species caught with trapping effort (Fig. 10). However, all curves (Fig. 10a and b) slightly level off with increase in number of individuals but did not reach an asymptote. Similarly, analysis of similarity (ANOSIM) revealed no significant differences in macro-invertebrate assemblages between abandoned kraals (Global R_{ANOSIM} = -0.019, P = 0.605) and control plots (Global R_{ANOSIM} = 0.12, P = 0.144).

5.3.4 Effect of abandoned kraals on functional diversity macro-invertebrates (combined)

There was a significant variation in mean FRic (t_{21}=2.850; P = 0.01) and FDiv (t_{21}=2.566; P = 0.018) between the abandoned kraals and control plots with the lowest means recorded in control plots (Fig. 11). However, no significant differences were recorded for FEve (t_{21}=0.777; P = 0.446) and FDis (t_{23}=2.012; P = 0.056) although FDis was marginally non-significant (Fig. 2).

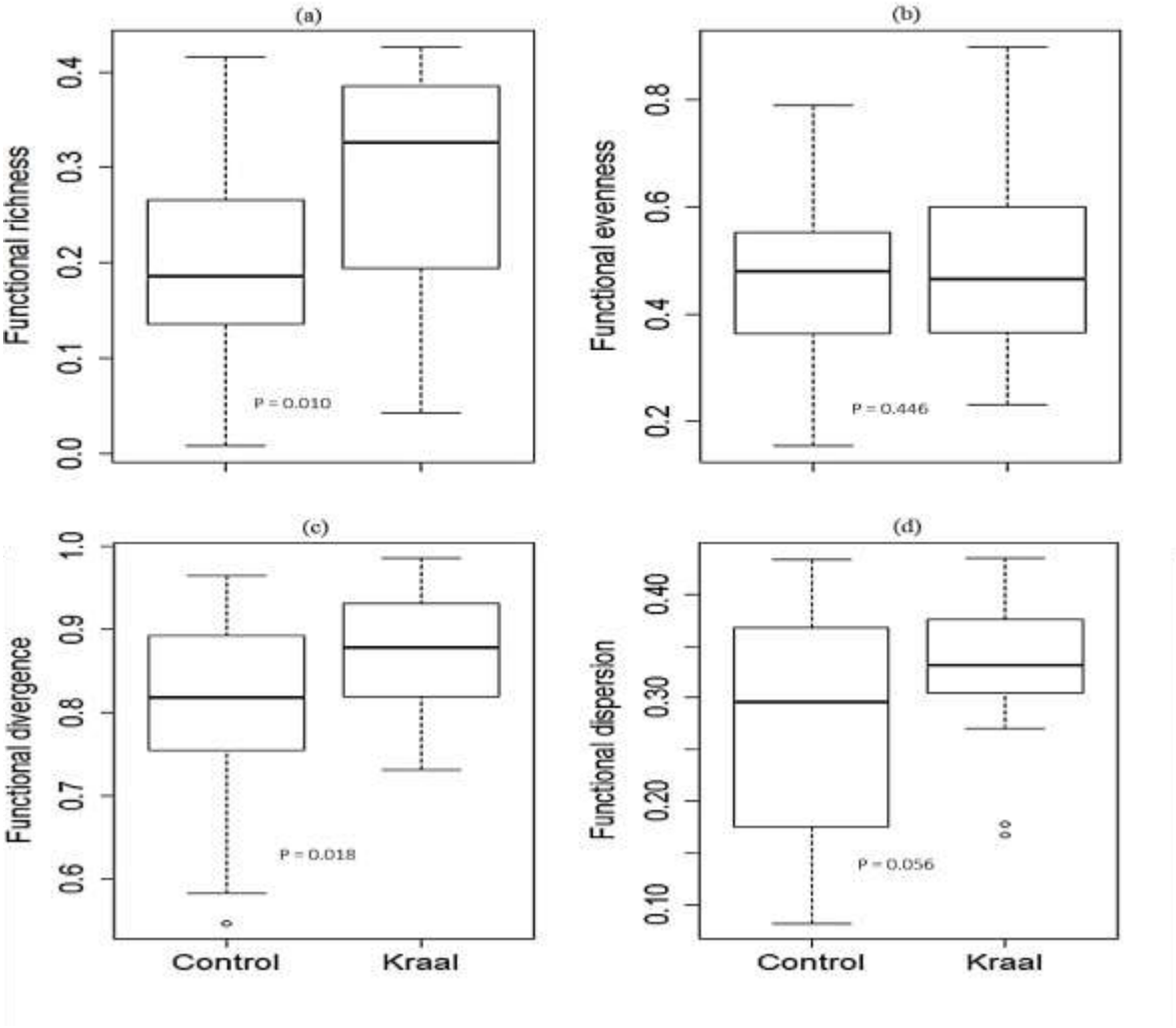

Figure 11. Functional diversity response of macro-invertebrates (combined above and belowground) between abandoned kraals and control plots in Save Valley Conservancy, Zimbabwe.

5.3.5 Functional diversity response of aboveground and belowground macro-invertebrates

Functional richness (FRic) of macro-invertebrates did not differ significantly between kraals and controls for aboveground (t_{10}=1.495; P = 0.167) while it was significantly higher on abandoned kraals (t_{10}=2.547; P = 0.034) for belowground (Fig. 12a). No significant variation (P>0.05) was recorded between abandoned kraals and controls for both aboveground and belowground invertebrates in FEve; FDiv and FDis (Fig. 12b-d).

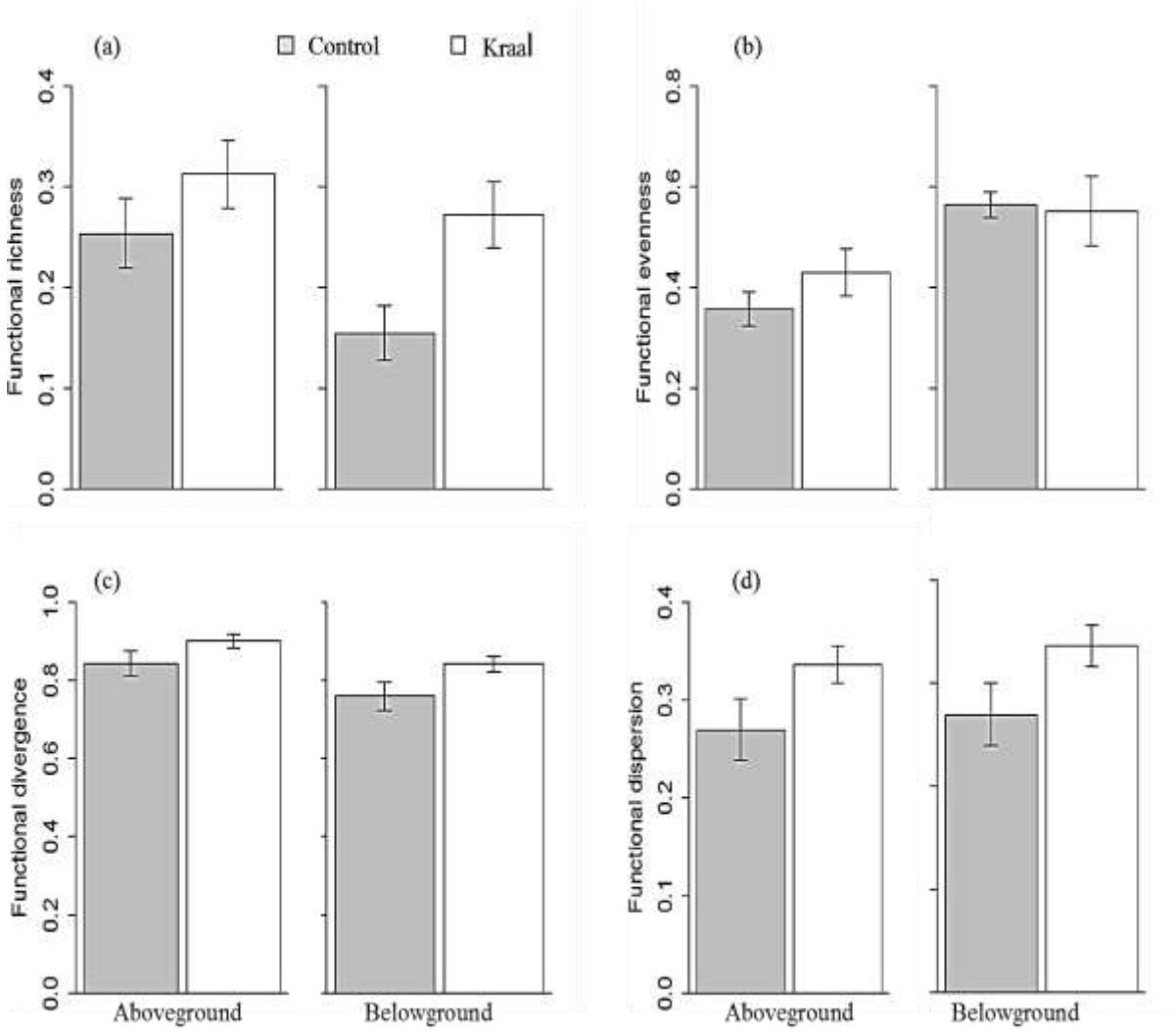

Figure 12. Functional diversity response of aboveground and belowground macro-invertebrates between abandoned kraals and control plots in Save Valley Conservancy, Zimbabwe.

5.3.6 Effect of abandoned kraals on functional response group (FRG) composition.

Unexpectedly, all functional response groups (relative abundances) showed no significant difference ($F_6 = 0.129$; $P > 0.05$) between abandoned kraals and control plots (Table 8). However, abandoned kraals had on average high values. Out of 10 functional response groups selected, FRG 6 (phytophagous with both legs and wings) and FRG10 (predacious with both legs and wings) were only found on abandoned kraals whereas FRG7 (phytophagous non-eusocial) was exclusive to the control plots (Appendix 2).

Table 8. Comparison of relative abundances of functional response groups (FRGs) between abandoned kraals and control plots in Save Valley Conservancy, Zimbabwe (mean ± standard error).

Functional response group	Kraal	Control	P-value
FRG1	3.95 ± 0.33	3.47 ± 0.37	0.972
FRG2	1.73 ± 0.66	1.39 ± 0.80	0.998
FRG3	1.50 ± 0.32	0.75 ± 0.41	0.992
FRG4	2.36 ± 0.27	2.00 ± 0.31	0.999
FRG5	2.79 ± 0.21	2.43 ± 0.31	0.977
FRG8	1.86 ±0.49	0.98 ± 0.69	0.999
FRG9	1.50 ±0.45	1.15 ± 0.48	0.999

5.4 Discussion

In our study, we predicted that functional diversity would be higher on nutrient-rich abandoned kraals than the surrounding savanna habitat. Contrary to our prediction, we found that functional evenness, divergence and dispersion of macro-invertebrate showed no response to the effect of abandoned kraals for both aboveground and belowground habitats. However, only

the functional richness of belowground macroinvertebrates responded positively on abandoned kraals. When aboveground and belowground macroinvertebrates were combined for kraals and control plots, larger values for functional richness were obtained for kraals compared with the control plots. The higher values for FRic, FDiv and FDis for combined above and belowground macroinvertebrates on abandoned kraals 20 years later suggest that they still have an effect on ecosystem processes.

5.4.1 Productivity of abandoned kraals

Our soil chemical results confirmed that abandoned kraals are nutrient-rich habitats (Kizza et al., 2010; Porensky et al., 2013; van der Waal et al., 2011) with improved plant productivity (herbaceous cover and biomass) than the surrounding savanna habitat (Muchiru et al., 2009; Veblen, 2012). This is explained by the persistence of residual nutrients from cattle dung which is probably being maintained by plant-soil-herbivore nutrient feedback system (van der Waal et al., 2011) whereby herbivores are attracted to nutritious forage on kraals thereby further enriching the site through excretion. Higher levels of soil N and P recorded on kraals is consistent with the findings of Veblen, (2012) who recorded N and P to be 3.8 and 6.8 times higher on abandoned kraals. A high herbaceous biomass and cover (surrogates of plant productivity) on abandoned kraals showed their positive response to limiting soil nutrients. This result is consistent with other findings from abandoned kraals in the semi-arid savanna (van der Waal et al., 2011; Veblen & Young, 2010; Young et al., 2013). Also, it was observed in this study that abandoned kraals were dominated by vigorous forbs with thick culms and branches which could have contributed to a high herbaceous biomass and cover.

5.4.2 Functional diversity

Results from our overall assessment of functional diversity between kraals and controls showed that FRic and Fdiv was high on abandoned kraals. This might suggest that abandoned kraals still exert a disproportionate number of ecosystem processes compared to the savanna matrix. However, against our prediction, FEve and FDiv showed a similar result between kraals and controls. These results concur with the findings of Audino et al. (2014) and Barragan et al. (2011) who attributed the lack of difference in FEve and FDiv to the identity of traits which may be influenced by the environment than the structure of the functional assemblage. Also, this may infer that kraals being sources of habitat heterogeneity which safeguard the ecosystems from environmental stochasticity, stability of the ecosystem can be compromised through competition (Decaëns, 2010). As explained by Audino et al. (2014), highly disturbed areas only supports tolerant species which makes them cluster and have an irregular distribution with their members in functional space.

Contrast analyses for aboveground and belowground habitats across sites revealed no significant differences which indicates a similarity and complementarity of functional roles between habitats (Bardgett & Wardle, 2003). On the other hand, our limited sampling adequacy (Fig. 10) could have underrepresented rare species with the missing functional groups (Mumme et al., 2015). It can also be attributed to the generalist feeding behaviour of the majority of macro-invertebrate species which can disperse randomly in the habitat matrix (Hooper et al., 2000). In this study, a 100m distance between kraals and savanna control plots could have been traversed during foraging and dispersal. These findings suggest that the two decade old disturbed habitat matrix has been recovering in terms of macro-invertebrate functional assemblages and the ecosystem is maintaining its stability. Interestingly, functional richness of belowground species was significantly higher on abandoned kraals probably because of limited

horizontal mobility of belowground macro-invertebrates (Doblas-Miranda et al., 2009). This may also suggest that the elevated soil nutrients and herbaceous productivity create a favourable micro-climate for belowground soil biota (Hooper et al., 2000). For instance the obligate soil, root and microbe feeders.

We recorded no significant variation in functional response group richness indicating that the ecosystem is in the process of maintaining its stability and resilience with an even distribution of functional groups. However, other functional response groups (FRG6: phytophagous and FRG10: predacious) appeared to be exclusive to abandoned kraals and FRG7 (phytophagous, non-eusocial) to savanna matrix owing to habitat specialisation by such species (Doblas-Miranda et al, 2009). According to Mumme et al. (2015), the frequency and intensity of disturbance might be so high that it results in diffuse ecological filtering which cause a random loss of species. This may result in susceptibility of species to extinction after a disturbance and ultimately the loss of several ecological functions (Barragan et al., 2011).

5.4.3 Conclusion

Abandonment of livestock areas can have serious implications on biodiversity and ecosystem processes, but the knowledge of how they affect the functional trait composition of macroinvertebrates is limited. Our study, for the first time, demonstrates that abandoned kraals in semi-arid savannahs have the capacity to increases the functional assemblages of macroinvertebrates as shown when belowground and aboveground species were combined. Functional diversity of belowground macroinvertebrates seems to exhibit a faster response to kraal abandonment than more mobile aboveground organisms, suggesting that their associated ecosystem services may take shorter to recover in response to land-use change. Although we lack time series data, we can confirm that nutrient-rich disturbed sites have the potential to

regain species and retain their ecosystem functionality, as shown by higher diversity on such sites in SVC.

5.5 Acknowledgements

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Appendix 2: Functional response groups of morphospecies sampled in abandoned kraals and control plots in Save Valley Conservancy. Ecosystem engineering SOMt&NC: soil organic matter transformation and nutrient cycling, LT: litter transformation, B: bioturbation. Dispersal capacity LW: legs and wings, LN: legs and no wings, NN: no legs and no wings.

Functional response group	Genus/ species	Feeding group	Ecosystem engineering	Eusociality	Dispersal capacity	Habitat specificity	Abundance	
							kraal	savanna
FRG1	*Archibracon serviellei*	*PARASITIC*	*SOMt&NC*	*Yes*	*LW*	*kraal*	1	-
FRG1	*Camponotus maculatus*	*OMNIVOROUS*	*SOMt&NC*	*Yes*	*LN*	*kraal and savanna*	17	5
FRG1	*Formicidae* sp.	*OMNIVOROUS*	*SOMt&NC*	*Yes*	*LN*	*kraal*	6	-
FRG1	*Hodotermes mossambicus*	*PHYTOPHAGOUS*	*SOMt&NC*	*Yes*	*LW*	*kraal and savanna*	19	8
FRG1	*Macrotermes michaelseni*	*PHYTOPHAGOUS*	*SOMt&NC*	*Yes*	*LW*	*kraal and savanna*	26	71
FRG1	*Messor capensis*	*OMNIVOROUS*	*SOMt&NC*	*Yes*	*LN*	*kraal and savanna*	7	25
FRG1	*Mutilla astarte*	*PHYTOPHAGOUS*	*SOMt&NC*	*Yes*	*LN*	*kraal*	2	-
FRG1	*Myrmicaria natalensis*	*OMNIVOROUS*	*SOMt&NC*	*Yes*	*LN*	*kraal and savanna*	161	68
FRG1	*Pachycondyla tarsata*	*OMNIVOROUS*	*SOMt&NC*	*Yes*	*LN*	*kraal and savanna*	275	75
FRG1	*Polyrhachis* sp.	*OMNIVOROUS*	*SOMt&NC*	*Yes*	*LN*	*savanna*	-	1
FRG1	*Tetraponera* sp.	*OMNIVOROUS*	*SOMt&NC*	*Yes*	*LN*	*kraal and savanna*	4	4
FRG10	*Anthia pachyoma*	*PREDACIOUS*		*No*	*LW*	*kraal*	2	-
FRG10	*Cheilomenes lunata*	*PREDACIOUS*		*No*	*LW*	*kraal*	2	-
FRG10	*Cypholoba alveolata*	*PREDACIOUS*		*No*	*LW*	*kraal*	1	-
FRG10	*Henosepilachna bifasciata*	*PREDACIOUS*		*No*	*LW*	*kraal*	1	-

FRG10	*Hoplocoryphella grandis*	*PREDACIOUS*		*No*	*LW*	*kraal*	1	-
FRG10	*Leptodena acanthoocephalum*	*PREDACIOUS*		*No*	*LW*	*kraal*	1	-
FRG10	*Mantidae* sp.	*PREDACIOUS*		*No*	*LW*	*kraal*	2	-
FRG10	*Pachylister caffer*	*PREDACIOUS*		*No*	*LW*	*kraal*	8	-
FRG10	*Philodicus* sp.	*PREDACIOUS*		*No*	*LW*	*kraal*	2	-
FRG10	*Poecilothais tetragramma*	*PREDACIOUS*		*No*	*LW*	*kraal*	1	-
FRG2	*Cormocephalus* sp.	*SAPROPHAGOUS*	*B*	*No*	*LN*	*kraal and savanna*	5	6
FRG2	*Odontopygidae* larvae	*SAPROPHAGOUS*	*B*	*No*	*LN*	*kraal*	4	-
FRG2	*Scolopendra morsitans*	*SAPROPHAGOUS*	*B*	*No*	*LN*	*kraal and savanna*	8	2
FRG3	Acarina larvae	*PREDACIOUS*		*No*	*LN*	*savanna*	-	1
FRG3	*Araneidae* juvenile	*PREDACIOUS*		*No*	*LN*	*kraal*	2	-
FRG3	*Corrinnidae*	*PREDACIOUS*		*No*	*LN*	*kraal*	4	-
FRG3	*Cubionidae*	*PREDACIOUS*		*No*	*LN*	*kraal*	8	-
FRG3	*Damon* sp.	*PREDACIOUS*		*No*	*LN*	*kraal*	2	-
FRG3	*Gnaphosidae* sp.	*PREDACIOUS*		*No*	*LN*	*kraal and savanna*	8	7
FRG3	*Heteropodidae*	*PREDACIOUS*		*No*	*LN*	*savanna*	-	1
FRG3	*Lycosidae* sp.	*PREDACIOUS*		*No*	*LN*	*kraal and savanna*	19	4
FRG3	*Opistophthalmus glabrifrons*	*PREDACIOUS*		*No*	*LN*	*kraal*	2	-
FRG3	*Palpares* sp.	*PREDACIOUS*		*No*	*LN*	*kraal and savanna*	2	1
FRG3	*Parabothus transvaalicus*	*PREDACIOUS*		*No*	*LN*	*savanna*	-	1
FRG3	*Salticidae* sp.	*PREDACIOUS*		*No*	*LN*	*kraal*	3	-
FRG3	*Selenopes* sp.	*PREDACIOUS*		*No*	*LN*	*kraal*	2	-
FRG3	*Solfugidae* sp.	*PREDACIOUS*		*No*	*LN*	*savanna*	-	1
FRG3	*Tarachodes* sp.	*PREDACIOUS*		*No*	*LW*	*savanna*	-	1
FRG3	*Thomisidae* sp.	*PREDACIOUS*		*No*	*LN*	*kraal and savanna*	1	2
FRG3	*Zodarridae* sp.	*PREDACIOUS*		*No*	*LN*	*kraal and savanna*	1	1
FRG4	*Adesmia schouteni*	*SAPROPHAGOUS*	*LT*	*No*	*LW*	*kraal and savanna*	31	22
FRG4	*Anachalcos convexus*	*SAPROPHAGOUS*	*LT*	*No*	*LW*	*kraal and savanna*	8	12

FRG4	*Anomalipus polymorphus*	*SAPROPHAGOUS*	*LT*	*No*	*LW*	*savanna*	-	2
FRG4	*Aphodius* sp.	*SAPROPHAGOUS*	*LT*	*No*	*LW*	*kraal and savanna*	1	1
FRG4	*Copris elpharon*	*SAPROPHAGOUS*	*LT*	*No*	*LW*	*kraal and savanna*	19	2
FRG4	*Endustomus parallelogrammus*	*SAPROPHAGOUS*	*LT*	*No*	*LW*	*kraal*	1	-
FRG4	*Eurychora* sp.	*SAPROPHAGOUS*	*LT*	*No*	*LW*	*kraal*	4	-
FRG4	*Kheper nigroaeneus*	*SAPROPHAGOUS*	*LT*	*No*	*LW*	*savanna*	-	1
FRG4	*Onitis fulgidus*	*SAPROPHAGOUS*	*LT*	*No*	*LW*	*kraal*	1	-
FRG4	*Onitis westermanni*	*SAPROPHAGOUS*	*LT*	*No*	*LW*	*kraal*	2	-
FRG4	*Phanerotoma arnoldi*	*SAPROPHAGOUS*	*LT*	*No*	*LW*	*kraal and savanna*	4	6
FRG4	*Phanerotoma scobicolle*	*SAPROPHAGOUS*	*LT*	*No*	*LW*	*savanna*	-	1
FRG4	*Psammodes virago*	*SAPROPHAGOUS*	*LT*	*No*	*LW*	*kraal*	4	-
FRG4	*Scarabaeidae* sp.	*SAPROPHAGOUS*	*LT*	*No*	*LW*	*kraal and savanna*	1	1
FRG4	*Schizonycha valida*	*SAPROPHAGOUS*	*LT*	*No*	*LW*	*kraal and savanna*	11	2
FRG4	*Stips dohrni*	*SAPROPHAGOUS*	*LT*	*No*	*LW*	*kraal*	1	-
FRG4	*Tenebrio molitor*	*SAPROPHAGOUS*	*LT*	*No*	*LW*	*kraal and savanna*	50	7
FRG4	*Trox sulcatus*	*SAPROPHAGOUS*	*LT*	*No*	*LW*	*kraal*	1	-
FRG4	*Zophosis mniszechi*	*SAPROPHAGOUS*	*LT*	*No*	*LW*	*kraal and savanna*	31	32
FRG5	*Acraea* larvae	*PHYTOPHAGOUS*		*No*	*LW*	*kraal and savanna*	16	7
FRG5	*Acrida* juvenile	*PHYTOPHAGOUS*		*No*	*LW*	*kraal and savanna*	1	3
FRG5	*Aspilocoryphus fasciativentris*	*PHYTOPHAGOUS*		*No*	*LW*	*kraal and savanna*	41	5
FRG5	*Belenois aurota*	*PHYTOPHAGOUS*		*No*	*LW*	*kraal and savanna*	2	7
FRG5	*Calodemas nickerli*	*PHYTOPHAGOUS*		*No*	*LW*	*kraal and savanna*	-	2
FRG5	*Carbula marginella*	*PHYTOPHAGOUS*		*No*	*LW*	*kraal and savanna*	60	5
FRG5	*Catacops melanostica*	*PHYTOPHAGOUS*		*No*	*LW*	*kraal and savanna*	5	5
FRG5	*Charaxes* sp.	*PHYTOPHAGOUS*		*No*	*LW*	*kraal and savanna*	2	2
FRG5	*Cletus* sp.	*PHYTOPHAGOUS*		*No*	*LW*	*kraal and savanna*	17	2
FRG5	*Crabonites equestris*	*PHYTOPHAGOUS*		*No*	*LW*	*kraal and savanna*	1	2
FRG5	*Dieuches armipes*	*PHYTOPHAGOUS*		*No*	*LW*	*kraal and savanna*	1	6

FRG5	*Dysdercus intermedus*	*PHYTOPHAGOUS*		*No*	*LW*	*kraal and savanna*	71	97
FRG5	*Geocnethus plagiata*	*PHYTOPHAGOUS*		*No*	*LW*	*kraal and savanna*	8	8
FRG5	*Lepidoptera* juvenile	*PHYTOPHAGOUS*		*No*	*LW*	*kraal and savanna*	20	7
FRG5	*Lygaeidae* sp.	*PHYTOPHAGOUS*		*No*	*LW*	*kraal and savanna*	3	2
FRG5	*Morphacris fasciata*	*PHYTOPHAGOUS*		*No*	*LW*	*kraal and savanna*	15	2
FRG5	*Nezara virudia*	*PHYTOPHAGOUS*		*No*	*LW*	*kraal and savanna*	1	1
FRG5	*Oedaleus* sp.	*PHYTOPHAGOUS*		*No*	*LW*	*kraal and savanna*	6	9
FRG5	*Oncopeltus famelicus*	*PHYTOPHAGOUS*		*No*	*LW*	*kraal and savanna*	25	22
FRG5	*Oxycarenus hyalipennis*	*PHYTOPHAGOUS*		*No*	*LW*	*kraal and savanna*	16	1
FRG5	*Pephricus* sp.	*PHYTOPHAGOUS*		*No*	*LW*	*kraal and savanna*	1	1
FRG5	*Piezomastax* sp.	*PHYTOPHAGOUS*		*No*	*LW*	*kraal and savanna*	21	6
FRG5	*Plagiodera caffra*	*PHYTOPHAGOUS*		*No*	*LW*	*kraal and savanna*	3	6
FRG5	*Scantius forsteri*	*PHYTOPHAGOUS*		*No*	*LW*	*kraal and savanna*	28	11
FRG6	*Acrida acuminata*	*PHYTOPHAGOUS*		*No*	*LW*	*kraal*	4	-
FRG6	*Aselgela ramulifera*	*PHYTOPHAGOUS*	*LT*	*No*	*LW*	*kraal*	3	-
FRG6	*Graptostethus servus*	*PHYTOPHAGOUS*		*No*	*LW*	*kraal*	1	-
FRG6	*Humbe tenuicornis*	*PHYTOPHAGOUS*		*No*	*LW*	*kraal*	3	-
FRG6	*Lamarkiana puntosa*	*PHYTOPHAGOUS*		*No*	*LW*	*kraal*	3	-
FRG6	*Mecostibia mopane*	*PHYTOPHAGOUS*		*No*	*LW*	*kraal*	1	-
FRG6	*Pentatomidae* sp.	*PHYTOPHAGOUS*		*No*	*LW*	*kraal*	5	-
FRG7	*Diploxys fallax*	*PHYTOPHAGOUS*		*No*	*LW*	*savanna*	-	1
FRG7	*Lamarkiana puntosa*	*PHYTOPHAGOUS*		*No*	*LW*	*savanna*	-	1
FRG7	*Orthoctha* sp.	*PHYTOPHAGOUS*		*No*	*LW*	*savanna*	-	4
FRG8	*Blattidae* juvenile	*OMNIVOROUS*		*Yes*	*LW*	*kraal*	5	-
FRG8	*Gryllidae* juvenile	*OMNIVOROUS*		*No*	*LW*	*kraal*	6	2
FRG8	*Hostilia* sp.	*OMNIVOROUS*		*Yes*	*LW*	*kraal and savanna*	13	5
FRG8	*Russipolia differens*	*OMNIVOROUS*		*No*	*LW*	*kraal and savanna*	7	1
FRG9	*Altractonotus mulsanti*	*PREDACIOUS*		*No*	*LW*	*kraal and savanna*	2	5

FRG9	*Carabidae* sp.	*PREDACIOUS*	*No*	*LW*	*kraal and savanna*	15	2
FRG9	*Dromica spectabilis*	*PREDACIOUS*	*No*	*LW*	*savanna*	-	2
FRG9	*Ligariella* sp.	*PREDACIOUS*	*No*	*LW*	*kraal and savanna*	3	2
FRG9	*Mylabris pollita*	*PREDACIOUS*	*No*	*LW*	*kraal and savanna*	3	2
FRG9	*Parena ferruginea*	*PREDACIOUS*	*No*	*LW*	*kraal and savanna*	2	7

CHAPTER 6

DISCUSSION, CONCLUSION AND RECOMMENDATIONS

6.1 Introduction

The main objective of this study was to assess and improve the understanding of how abandoned kraals as sources of nutrient heterogeneity influence the interaction of plant assemblages, herbivory and macro-invertebrate community. In African savannas, vegetation structure, composition and distribution is chiefly determined by nutrient availability, herbivory, fire and rainfall (Sankaran et al., 2005; Scholes & Archer, 1997). Understanding how nutrient patchiness controls habitat productivity and influences animal assemblages and other guilds of living organisms in dystrophic African savannas is key to the successful management of disturbed habitats. This study, therefore, brings an understanding on how abandoned kraals influence the interaction of vegetation structure, composition and productivity, ungulate herbivory and taxonomic and functional diversity of macro-invertebrates. Chapter 3, assessed the influence of abandoned kraals on plant structure and composition, forage quality and quantity, ungulate herbivory and further explored their interaction. Chapter 4, analysed the influence of abandoned kraals on diversity and abundance of macro-invertebrates. Chapter 5, analysed the role of abandoned kraals in influencing the functional diversity of macro-invertebrates. Each chapter has brought new empirical understanding on how abandoned kraals embedded in a lower-nutrient savanna habitat has significance influence on plant development, herbivory and macro-invertebrate (taxonomic and functional) assemblages. In this final chapter, the major findings of the chapters are synthesized in order to have a better understanding of the ecological implications of abandoned kraals.

6.2 Ecological implications of abandoned kraals

6.2.1 Soil characteristics

Abandoned kraals are long-term sources of nutrient heterogeneity in semi-arid savannas (Kizza et al., 2010; Muchiru et al., 2009; van der Waal et al., 2011)**.** Results in Chapter 3 indicate that the abandoned kraals (22 years after) are still nutrient-rich compared to the surrounding savanna matrix (*e.g.* Table 1). Abandoned kraals were laden with residual nutrients from dung and urine deposition during the cattle ranching era and thereafter soil nutrients were maintained by a positive feedback loop of animals feeding at these sites, dropping dung and urine (Augustine et al., 2003; Grant & Scholes, 2006; van der Waal et al., 2011). The glade-like characteristic of abandoned kraals make them the preferred feeding sites by ungulate herbivores as it offers an improved predator detection, thereby further enriching the sites through nutrient importation and deposition. On the other hand, continuous deposition of dung and urine creates a favourable organic environment for macro and micro-invertebrates which accelerate nutrient cycling. For instance, soil N and P were 1.7 and 1.5 times high on abandoned kraals (Table 1). Although concentrations of soil N, P, K and Ca were significantly high on abandoned kraals, they were much lesser than in other studies in the savanna (Kizza et al., 2010; van der Waal et al., 2011; Veblen, 2012) probably due to the effect of kraal age and differences in geological formations.

6.2.2 Vegetation structure and composition

The results from Chapter 3 clearly indicated that the 22-year old abandoned kraals did not influence Shannon Wiener plant diversity (Table 2). This is an interesting result since nutrient heterogeneity has been demonstrated to influence plant assemblages in other studies within the savannas (Du Toit et al., 2003; Sankaran et al., 2005; Scholes & Archer, 1997; van der Waal, 2010). As explained by the Intermediate Disturbance Hypothesis (Connell, 1978), the increased

concentration of soil nutrients on abandoned kraals could be resembling a moderate disturbance where most plant species had an equal chance to utilise the resources than in the nutrient-poor savanna habitat. However, woody species richness was high outside abandoned kraals explaining the poor woody recruitment inside kraals because much of the trees were cut during construction and growth suppressed by animal activity. Grasses and forbs had a similar composition inside and outside kraals, suggesting that the abandoned kraals have naturally recovered to stability in terms of herbaceous composition. In terms of herbaceous productivity, it was clear that abandoned kraals were still more productive sites with high forb and grass covers (Table 2). It has been demonstrated that herbaceous vegetation benefited more to resource patchiness on a fine scale than woody species (van der Waal, 2010) because of their small rooting range and high nutrient uptake capacity. Therefore, tree-grass interactions (Scholes & Archer, 1997) may in part explain why woody density was significantly low inside kraals as grass tend to be initially more competitive than trees in nutrient uptake.

6.2.3 Forage properties and herbivory

This study found that herbaceous productivity (biomass and plant cover) was twice high on abandoned kraals indicating a positive response to the increase in limiting soil nutrients. In a relatively nutrient-poor savanna ecosystem, nutrient hotspots such as abandoned kraals, provide high quality forage with scarce nutrients essential for animal production during active growing stages (Augustine et al., 2003; Grant & Scholes, 2006; van der Waal et al., 2011). The forage analyses done on commonly found forage species (woody, grasses and forbs) (Chapter 3, Fig 3) revealed that grasses and trees from abandoned kraals contain significantly high amounts of foliar N and P than those from savanna controls. Unexpectedly, forb species showed no significant differences in forage nutrition between kraals and controls. Generally, all forage species found on abandoned kraals were high in foliar K, Ca, Mn, Zn and B. It is

interesting to note that forb species had the least amount of foliar nutrients recorded for both sites among the forage species (Fig 3) and less preferred by herbivores (Fig 2b) probably due to high accumulation of plant anti-nutritional factors or less nutrient returns to an animal (Ball et al., 2001). Considering the interactions between forage properties (quality, productivity and diversity) and herbivory (Chapter 3), diversity, basal cover and foliar N had the significant correlations with selected forb species. Moreover, grass biomass had a significant interaction with selected grass species (Fig 4). Contrary to our hypothesis, plant diversity and grazing percentage played a less significant role in explaining the interaction between forage properties and herbivory.

6.2.4 Diversity and abundance of macro-invertebrates

The results in Chapter 4 clearly show that abandoned kraals influence the richness of macro-invertebrates. It was expected that improved aboveground herbaceous productivity and elevated soil nutrients on abandoned kraals would increase the richness of aboveground and belowground macro-invertebrates respectively. Both below and aboveground macro-invertebrate richness was significantly higher on abandoned kraals than on control plots demonstrating the favourability of such a nutrient-rich microhabitat to a variety of macro-invertebrate species which favours habitats with good quality and quantity of feed resources (Doblas-Miranda et al., 2009; Decaëns et al., 1998). Eusocial macro-invertebrates *e.g.* termites, ants and bugs were dominant on both kraals and controls (200m apart). However, no significant difference was recorded for abundance of aboveground macro-invertebrates between kraals and controls. This was explained by the fact that aboveground species have increased horizontal mobility and dispersal capacity as they forage over long distances and swarming of new reproductives (Doblas-Miranda et al., 2009). The distance between kraals and controls (200m) could have been shorter to be easily traversed by most eusocial insects, thereby

increasing the species mix. Macro-invertebrate assemblages on aboveground and belowground habitat compartments respond differently to habitat heterogeneity (Hooper et al., 2000; Wardle et al., 2004; Doblas-Mirandaet al., 2009). Aboveground species are mainly affected by the dynamics in herbaceous productivity whereas belowground species are affected by variations in soil productivity (Hemerik & Brussaard, 2002). In terms of diversity (Shannon-Wiener and Hill N1), aboveground macro-invertebrates did not respond to increased herbaceous productivity. This is contrary to our hypothesis in Chapter 4. This is attributed to the small size of kraals (100m x 100m) which can be easily straddled by most aboveground species from both the kraal and the control. Belowground species on abandoned kraals were significantly diverse. This is attributed to their limited horizontal movement (Doblas-Miranda, 2007) and probably the presence of high microbial biomass on nutrient-enriched soils (Decaëns et al., 1998). Also, the belowground species could have favoured the abandoned kraals because of high herbaceous cover which provides a good thermal cover. For aboveground taxa, phytophagous and predacious ants had a close association with plant variables (Fig 7) whereas for belowground taxa, Myriapods, Coleopterans and Isopterans had a positive relationship with limiting soil N, P, K, and organic C (Fig 8). It can be suggested that the abandoned kraals (22 years later) in SVC have an influence on diversity of belowground macro-invertebrates. This is important since macro-invertebrates are found at the bases of food chains and food webs, alteration of their assemblage structure has serious consequences on ecosystem functioning.

6.2.5 Functional diversity of macro-invertebrates

A fundamental goal in disturbance ecology is to understand how biodiversity changes can have implications on the stability and resilience of natural ecosystems (Huston, 2014; Pey et al., 2014). Chapter 4, found that increased soil and herbaceous productivity on abandoned kraals

(Chapter 3) influence richness and abundance of macro-invertebrates. It is argued that taxonomic diversity responses must be complemented with a functional approach (trait-based) in order to better explain the impact of a disturbance on ecosystem functioning (Cole et al., 2006; Mumme et al., 2015; Petchey & Gaston, 2006). Thus, Chapter 5 looked at the influence of abandoned kraals on functional diversity of macro-invertebrates complementing the taxonomic diversity response in Chapter 4. Comparisons between abandoned kraals and nearby savanna controls revealed that an overall response in functional richness (FRic) and functional divergence (FDiv) were significantly high on abandoned kraals. This may suggest that these areas are nutrient-rich thus exerting a disproportionate number of ecosystem processes compared to the savanna habitat matrix. However, contrast analyses for belowground and aboveground habitats showed that only FRic had a significant difference for belowground habitat and a no significant differences for FEve, FDis and FDiv. Generally, a similar result in functional diversity response on above and belowground habitats is explained in part by our limited sampling adequacy (Fig 10) that could have underrepresented rare species with the missing functional groups (Mumme et al., 2015). Also, the majority of the macro-invertebrate species recorded in this study can disperse randomly within the savanna matrix which was only 100m away from the kraals, thereby increasing the chance of being caught within the matrix. They are indications that the ecosystem is in the process of maintaining stability and resilience as there were no significant variations in functional response group (FRG) richness between abandoned kraals and control plots (Table 8). However, some FRGs were exclusive to abandoned kraals (Appendix 2) owing to habitat specialisation (Doblas-Miranda, 2007) and probably diffuse ecological filtering which cause a random loss of species (Mumme et al., 2015). This scenario may result in susceptibility of species to extinction after a disturbance and ultimately the loss of several ecological functions (Barragan et al., 2011).

6.3 Scientific relevancy

This study has contributed scientific knowledge on the ecology of abandoned kraals in a number of ways. First, from the foregoing discussion it can be noted that the two decade abandoned kraals still have an important influence on soil nutrient concentrations. This is in line with previous studies which have demonstrated that on abandoned kraals soil nutrients persist for decades (Kizza et al., 2010; van der Waal et al., 2011; Young et al., 1998). This study has found that aboveground herbaceous productivity increase with an increase soil nutrient concentrations. However, it is observed that herbaceous composition did not respond to soil nutrient productivity which is contrary to the productivity-diversity hypothesis (Fridley et al., 2012; Grime, 1973). Therefore, it is suggested that the two decade abandoned kraals has little influence on herbaceous vegetation composition. In terms of forage quality and herbivory, foliar nutrients were significantly higher for grasses than forbs and grazing was high on abandoned kraals. This proved the foraging theory (Pyke, 1984) which states that herbivores select feed which gives them high fitness pay-off (Augustine et al., 2003; Grant and Scholes, 2006).

Second, it is demonstrated for the first time that abandoned kraals influence taxonomic richness and diversity of macro-invertebrates. This result corroborates findings of other studies on nutrient-rich habitat patches (Ayuke et al., 2009; Doblas-Miranda et al., 2008; Hemerik & Brussaard, 2002). However, assessment of above and belowground habitats showed that only the belowground taxa is affected significantly by nutrient patchiness. Thus, it is deduced that belowground taxa are more vulnerable to resource heterogeneity. Third, this study contributed to scarce information regarding the functional response of macro-invertebrates to nutrient heterogeneity. Generally functional diversity increased with increasing soil and plant variables (substrate). Results of contrast analyses by habitat compartment showed that abandoned kraals had no influence on functional stability and resilience of both the aboveground and

belowground taxa. This result must be treated with caution as my sampling was limited to one season and specific methods.

The major findings of this study are summarised in the hypothetical model (Fig 13) which shows how abandoned kraals as structurally open patches (high density of herbaceous than woody species) enriched with residual nutrients serve as a foci of aboveground macro-invertebrates and ungulate herbivores. Consequently, nutrient cycling is improved through deposition of excreta and the action of belowground macro-invertebrates. Ungulate herbivores are attracted to the kraals as open habitats with improved predator detection thereby enriching them with dung and urine. This result in growth of high quantity and quality of grass forage which then incentivise herbivores to continuously utilise the habitat. At the same time, aboveground invertebrates are attracted to the high quality and quantity of vegetation and other organic substrates while the improved soil physio-chemical properties and herbaceous cover attracts belowground invertebrates which further increase the nutrient cycling rates.

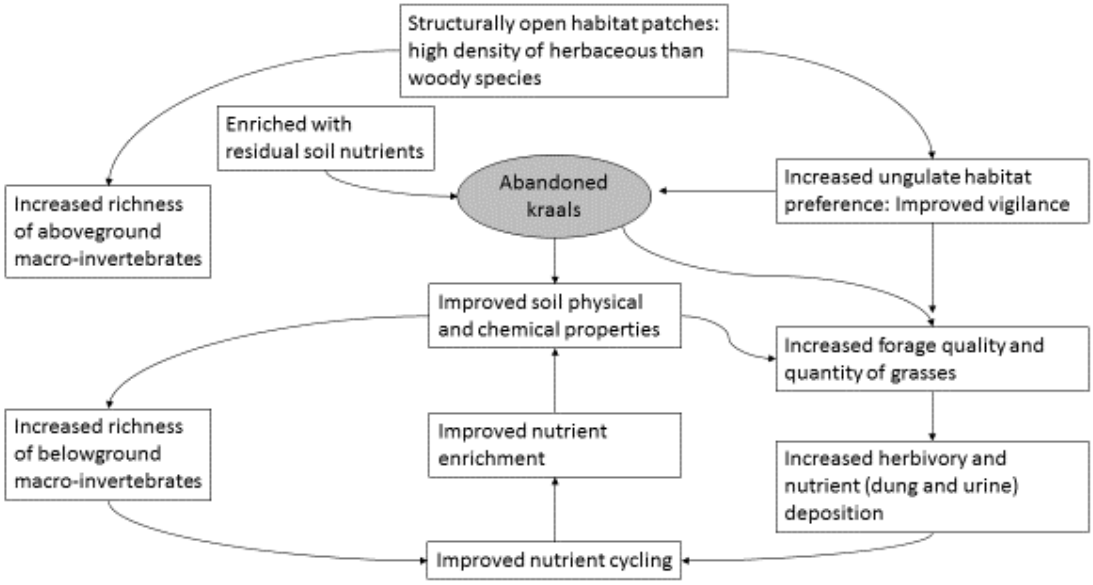

Figure 13. A hypothetical model explaining how after abandonment the cattle kraals remained as structurally open areas enriched with residual nutrients.

6.4 Societal relevancy

This study results suggest that creation and abandonment of cattle kraals have the potential to create long term habitat patches with disproportionately high nutrient loads persisting for decades in the soil. Also, abandoned kraals harbour high biomass of palatable forage at a time when natural pastures have declined in resource value. Thus, there is need to harness the harvest of organic manure as a soil amendment in dystrophic agro-ecosystems. The nutrient-rich grass forage can be harvested as a ready source of animal feed in agro-pastoral systems. Lastly, a good conservation practice of abandoned kraals ensure that soil is kept fertile being maintained by the action of belowground invertebrates.

6.5 Management implications

Improving the understanding on how anthropogenic disturbances can have far reaching consequences on biodiversity and ecosystem functioning is key to successful management of

disturbed habitats (Riginos et al., 2012). This study contributes new information to the ecology of nutrient hotspots in semi-arid African savannas which is important for the management of conservation areas.

First, abandoned kraals can serve as long-term nutrient rich patches in a low nutrient savanna landscape thus having implications on plant and animal assemblages (Grant & Scholes, 2006; van der Waal et al., 2011). From the results in Chapter 3, nutrient-rich forage growing on abandoned kraals can be incorporated into management plans as they serve as feed reserves for animal nutritional requirements in the dry season. The attraction of herbivores to abandoned kraals in search of nutritious feed (Augustine et al., 2003) and an open habitat spaces (Riginos & Grace, 2008) can be used as an opportunity in wildlife tourism and safaris who are interested in animal distribution.

Second, nutrient patchiness can have implications on richness and abundance of macro-invertebrates (Doblas-Miranda et al., 2009; Warui, 2004). To our knowledge, macro-invertebrates are rarely considered in the management plans of many protected areas in Zimbabwe despite their key roles in ecosystem functioning (Lavelle et al., 1997). Its high time managers incorporate macro-invertebrates in ecological planning and monitoring.

Third, in monitoring of biodiversity responses after a disturbance, ecologists should also factor in the functional responses as they determine the stability and resilience of the affected ecosystem (Díaz & Cabido, 2001). Results in Chapter 4 showed that the ecosystem has become stable in increase of macro-invertebrate species diversity after 22 years of disturbance despite that taxonomic diversity was significantly influenced.

Fourth, wildlife managers can adopt a holistic management where cattle and wildlife can be kept together and have mobile kraals for livestock fertilising the range. This is suitable for ranges with no other bovines and dangerous game.

6.6 Conclusion

In conclusion, results provide evidence that abandoned kraals are drivers of a habitat-scale heterogeneity with a potential to influence vegetation structure and composition, herbivory and macro-invertebrate assemblages. The study have shown that on abandoned kraals soil nutrients can persist for a long time which results in increased herbaceous productivity. Contrary to the productivity-diversity hypothesis (Fridley et al., 2012; Grime, 1973), after 22 years of abandonment, plant diversity was similar across the habitat matrix. Abandoned kraals support forage of high quality that has resulted in increased herbivory. These findings support the optimal foraging theory (Pyke, 1984) which states that animals favour to feed on high quality forage that maximises their net energy intake per foraging time. Among the herbaceous forage species, grasses were more nutritious and highly favoured by herbivores than forb species. A significant influence of abandoned kraals was shown in taxonomic richness of macro-invertebrates although contrast analyses only showed a significant response in diversity for the belowground macro-invertebrates. Lack of variation in FRGs between sampling sites indicate that the ecosystem is in the process of maintaining its stability and resilience. Considering the potential influence of nutrient-heterogeneity at finer scales on ecosystem processes and functioning in the savannas (Du Toit et al., 2003; Scholes, 1990), the findings of this study provide insightful information to ecologists and managers to incorporate nutrient hotspots in their management strategies.

6.7 Recommendations

- From this study, it is recommended that abandoned kraals be incorporated in habitat management plans as they serve as nutrient-hotspots for a diversity of flora and fauna
- Future studies should explore the spatio-temporal links between herbivory and forage species (grasses vs forbs) on high nutrient patches in a controlled exclusion experiment.
- Some peculiar plant species found on abandoned kraals are of the invasive nature, therefore, the role of abandoned kraals in propagation of invasive species must be explored.
- Since sampling effort on macro-invertebrates did not reach the sampling adequacy (Fig 10), longer sampling period is recommended (*e.g.* 24 months) using a variety of sampling techniques.
- A further research is needed on abandoned kraals to ascertain the sensitivity to resource heterogeneity of every individual taxa at different spatio-temporal scales.
- Taxonomic checklists of plants and macro-invertebrates on abandoned kraals and the surrounding habitat must be continuously updated for future studies in Save Valley Conservancy.

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