

CHAPTER 3 BIOGEOGRAPHICAL DISTRIBUTION PATTERNS OF THE BOTSWANA DUNG BEETLE FAUNA IN SOUTHERN AFRICA AND THE LOCAL BIOGEOGRAPHICAL COMPOSITION OF ASSEMBLAGES ACROSS THE BOTSWANA KALAHARI

Introduction

The geological processes and climatic oscillations during the Pliocene and Pleistocene have substantially influenced the African fauna and flora (Vrba, 1985; Linder, 2003). Chapters 1 and 2 have provided background information on the development of the Kalahari sands as a physical barrier and the aridity as a filter of savanna elements centred in the moist regions (Wright, 1978). The increasing aridity to the SW Kalahari is paralleled by changes in vegetation physiognomic structure (Scholes *et al.*, 2004; Ringrose *et al.*, 2002) and mammal assemblages that in turn would have affected other species that depend on them through changes in available resources. The present Kalahari basin environmental setting of the xeric and mesic ecoregions (Olson *et al.*, 2001) has potential effects on past lineage turnover (Vrba, 1985) and the current biogeographical patterns may reflect this past history.

Dung beetles are essentially good indicators of biogeographical patterns (Davis, 1997; Davis & Scholtz, 2001). They have a long history of association with mammal dung (Davis, 2001; Davis & Scholtz, 2002) and respond to microhabitat variations (Davis, 1996). In southern Africa there are *ca.*582 species of dung beetles occurring south of 15° S (Doube, 1991; Davis, 1997). Most species have broad distributions in a wide range of habitats (Davis *et al.*, 2009; Scholtz *et al.*, 2009) and a few species have restricted distributions (Davis, 2002). A substantial body of evidence has linked these distribution patterns to gradients in climate, altitude, soil and vegetation type or indigenous large mammal diversity and distribution (Davis, 1997; Davis & Scholtz, 2001, Scholtz *et al.*, 2009). Although several recent studies have documented faunal biogeographical compositions across the Kalahari basin (Barker, 1993; Davis, 1997; Prendini, 2005) and along the Karoo/Kalahari ecotones

(Davis & Scholtz, 2004; Davis *et al.*, 2008) some of these studies were undertaken with limited data for Botswana faunas (Davis, 1997; Prendini, 2005).

The present study examines biogeographical composition of dung beetle assemblages surveyed within the Kalahari basin across a climate gradient using an improved data set. It was hypothesized that the species distributions would classify into two major groups, NE savanna and SW Kalahari centred taxa (Davis, 1997; Davis & Scholtz, 2004; Davis *et al.*, 2008). It was expected that the results would provide some support for the hypothesis that the Kalahari deep sands act as a geographical barrier to many non-psammophilous savanna species and as filter for those psammophilous species intolerant of increasingly more arid conditions. This would account for the species turnover (Chapter 4) and endemism to the southwest demonstrated by Davis (1997).

3.2. Analytical Methods

3.2.1. Biogeographical composition of the Botswana dung beetle fauna

Multivariate techniques were used to determine the biogeographical distribution patterns shown by 140 dung beetle species recorded across the Botswana Kalahari basin. A data matrix was constructed using unpublished Southern African data from the former collection of the Australian CSIRO Dung Beetle Research Unit (now part of the National Collection of Insects, Pretoria, South Africa) and published records (Scholtz & Howden, 1987; Steenkamp & Chown, 1996; Davis *et al.*, 2003). The data matrix comprised 140 species by the number of degree squares occupied by each species in 25 southern African climate types (Fig 3.1). Before analysis for biogeographical patterns, the 140 x 25 data matrix was fourth-root-transformed to normalize the data and converted to a correlation matrix for 140 species. The matrix was subjected to factor analysis by STATISTICA release 9 (StatSoft Inc., 1994 - 2005) using principal components as the method of factor mining. Biogeographical clusters of species were defined at the default factor loading of 0.7 or greater.

Hierarchical analysis of oblique factors was conducted on the principal components factor analysis. The technique first rotates ordination axes through defined clusters, which has the effect of increasing the coalescence of data points around each factor and maximizing between cluster variance. A second ordination is conducted on the resulting ordinate values for the defined clusters. This generates primary factors (variance unique to a cluster) and secondary factors (variance shared between clusters). Regressions of these extended orthogonal factors on the original oblique factors generate a Pearson's r correlation coefficient. Multiplying these r values generate r^2 values (coefficient of determination), which represent the decimal proportion of variance accounted for by each extended factor within each cluster.

A further ordination technique, multi-dimensional scaling (MDS) (Primer v.5) was used to determine if similar results are obtained using a different analytical method.

The Proportional biogeographical composition of species abundance was determined for each of the five bait types for the six study areas. Cross-tabulation tables with goodness of fit tests (<http://home.ubalt.edu/ntsbarsh/Business-stat/otherapplets/Catego.htm>) were used to determine any significant difference between the biogeographical compositions of different study areas.

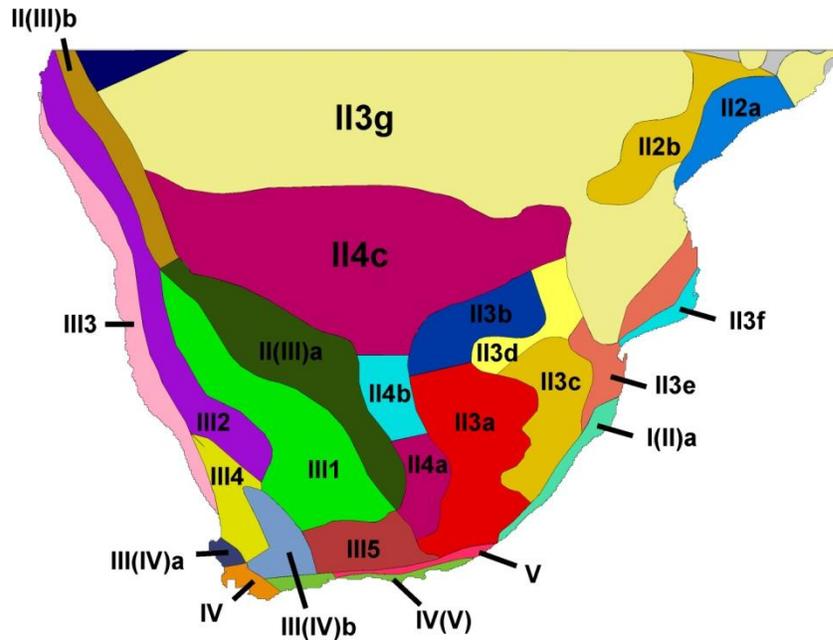


Figure 3.1. A map of southern Africa showing 25 Climate types defined by Walter and Lieth (1964)

3.3. Results

3.3.1. Influence of sub continental-scale factors on the species recorded in the survey area

Both ordination analyses yielded similar patterns of species group separation (Figs 3.2, 3.3). Four principal biogeographical groups were defined using factor analysis, plus one other group that comprised poorly recorded species (Fig. 3.2). This group classification was imposed on the MDS ordination plot to demonstrate the similarity in patterns (Fig. 3.3). The mostly high coefficient of determination values (r^2) for the correlation between oblique factors and the shared extended factor in Table 3.1., suggest a great deal of overlap between most clusters except cluster 2. The higher r^2 value for the correlations between oblique factor 2 and extended primary factor 2 indicates a more strongly defined unique character of biogeographical separation for that cluster. This cluster group contributes by far the greatest proportion of individuals to the faunas in the southwest of Botswana (Table 3.2.).

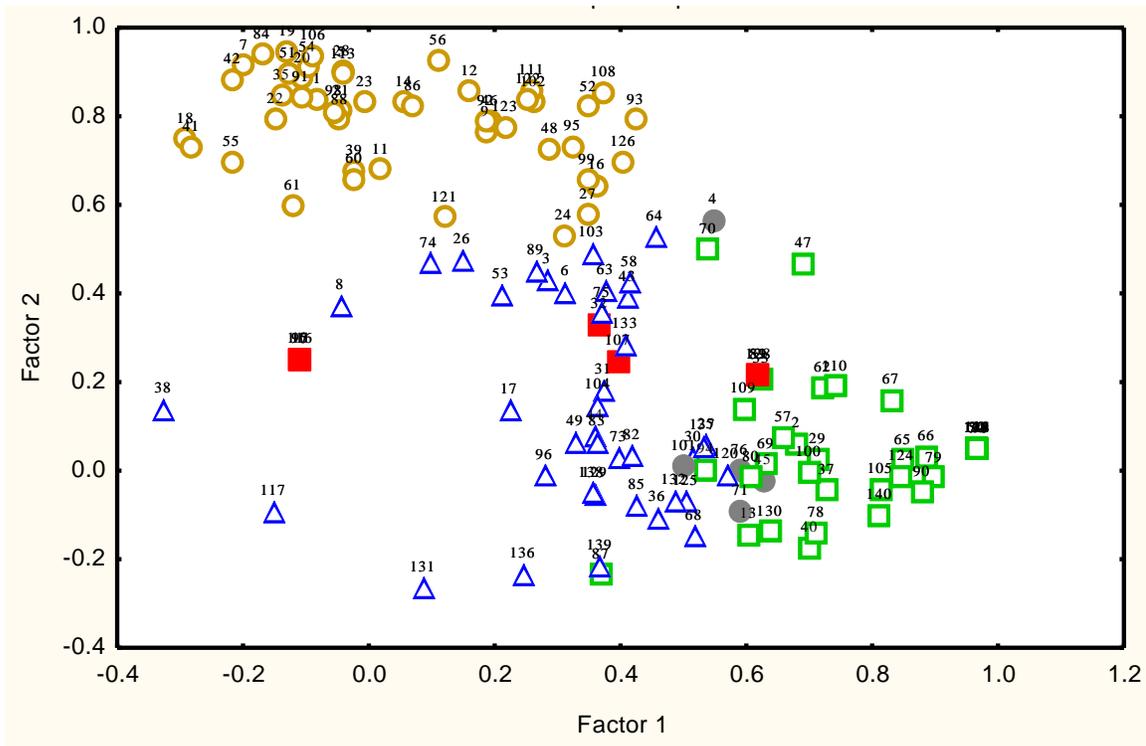


Figure 3.2. Ordination plot of species distributions in southern Africa derived from Factor Analysis (Cluster 2 = southwest bias (open circle), Cluster 4 = widespread/northeast (closed circle), Cluster 3 = widespread (triangle), Cluster 1 = northeast bias (open square), Cluster 5 = poorly recorded (closed square) (See Appendix A4 for key to species numbers)

The maps of overall distribution pattern of each species group in southern Africa, mostly suggest a great deal of spatial overlap (Fig. 3.4.). This is implicit in the results shown by Table 3.1 (see high r^2 values for correlations between oblique factors and the shared extended orthogonal factor in 3 out of 4 cases). Only Cluster 2 is shown to have a more clearly defined biogeographical character by the high r^2 for the correlation between the oblique and primary extended factor P2. In the maps, the relative centring of the cluster groups are probably obscured as some data points represent only one species record whereas others represent many species. The ordination plots, however, show clear group separations (Figs 3.3., 3.4.). The relative positioning of these cluster groups reflect their biogeographical pattern centred either to the northeast or southwest with widespread species occupying the intervening ordinal space.

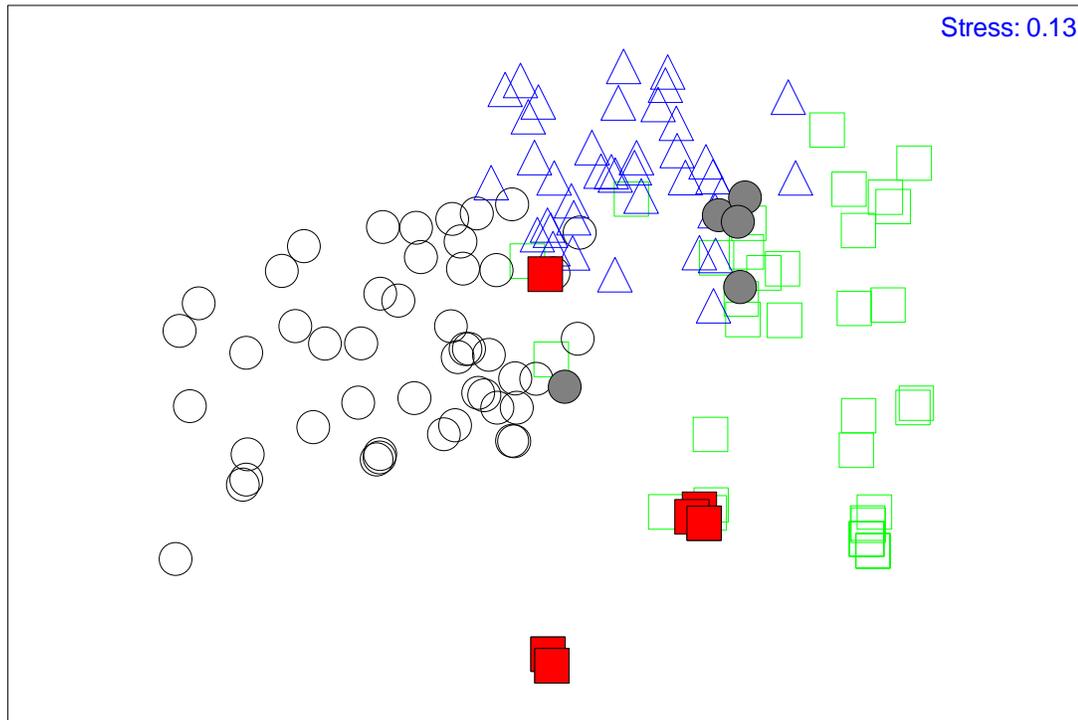


Figure 3.3. MDS ordination plot for five biogeographical clusters of species (Cluster 2 = southwest bias (open circle), Cluster 4 = widespread/northeast (closed circle), Cluster 3 = widespread (triangle), Cluster 1 = northeast bias (open square), Cluster 5 = poorly recorded (closed square))

The clusters of species showing widespread, northeast, or southwest biogeographical bias showed contrasting patterns of proportional representation across the sampling sites in the Kalahari. Species with a widespread / northeast or northeast bias showed a sharp decline in proportional abundance to the southwest whereas species with a southwest bias steadily increased (Table 3.2.). The proportional abundance of widespread species was high in the northeast savanna (Chobe) and in the transitional zone (northeast edge of the Kalahari at Khutse) (Table 3.2.).

The proportional biogeographical compositions of species attracted to each bait type largely reflected the general trends across the study areas (Table 3.2.) although there was a great deal of variation to the northeast (Table 3.3., Appendix 3.3). In terms of proportional abundance, species showing widespread/northeast or northeast biogeographical bias were,

again, principally centred in the more mesic northeast savanna (Chobe, Savuti). Those showing southwest biogeographical bias were well represented from the arid southwest to the southwest of the more mesic savanna (SW-Kalahari to Savuti) but mostly declined in representation to the northeast (Table 3.3). Those showing widespread biogeographical distribution were centred in the northeast of the savanna and northeast of the Kalahari (Chobe, Khutse). Also there was a slight variation in biogeographical composition between bait types in the NE although Kalahari endemics dominated all bait types in the SW (typified by low S.D.). Three to four patterns were well represented in Chobe and Savuti, two in NC-Kalahari and Khutse, and only one in Mabuasehube and SW-Kalahari, thus showing reduction in biogeographical diversity to the SW (Tables 3.2, 3.3).

Table 3.1. Correlations between oblique factor loadings (varimax-normalized rotated) and extended factors derived from hierarchical analysis of oblique factors from the biogeographical analysis (results for Cluster 5 omitted = poorly recorded species)

Extended factors	Correlation coefficient r and coefficient of determination (r^2)			
	Cluster 1 Northeast -bias	Cluster 2 Southwest - bias	Cluster 3 Widespread	Cluster 4 widespread/northeast
Shared factor (S1)	0.78 (0.61)	0.49 (0.24)	0.85 (0.72)	0.73 (0.54)
Primary factor (P1)	0.62 (0.39)	0.0	0.0	0.0
Primary factor (P2)	0.0	0.87 (0.76)	0.0	0.0
Primary factor (P3)	0.0	0.0	0.53 (0.28)	0.0
Primary factor (P4)	0.0	0.0	0.0	0.68 (0.46)

Table 3.2. Overall proportional biogeographical composition (species clusters defined in Fig. 3.1.) at the six study areas in Botswana

Biogeographical group	Percentage abundance					
	Chobe River	Savuti	NC-Kalahari	Khutse	Mabuasehube	SW-Kalahari
Widespread/northeast	33.84	11.99	4.91	0.02	0.05	0.0
Widespread	32.62	11.31	11.14	31.48	1.06	0.71
Northeast - bias	19.92	35.06	2.98	1.28	0.07	0.0
Southwest - bias	13.59	41.44	80.87	66.79	98.71	99.29
Poorly recorded	0.03	0.21	0.10	0.43	0.11	0.0
Total abundance	44446	13980	6949	26316	18819	12987

values > 10 % highlighted

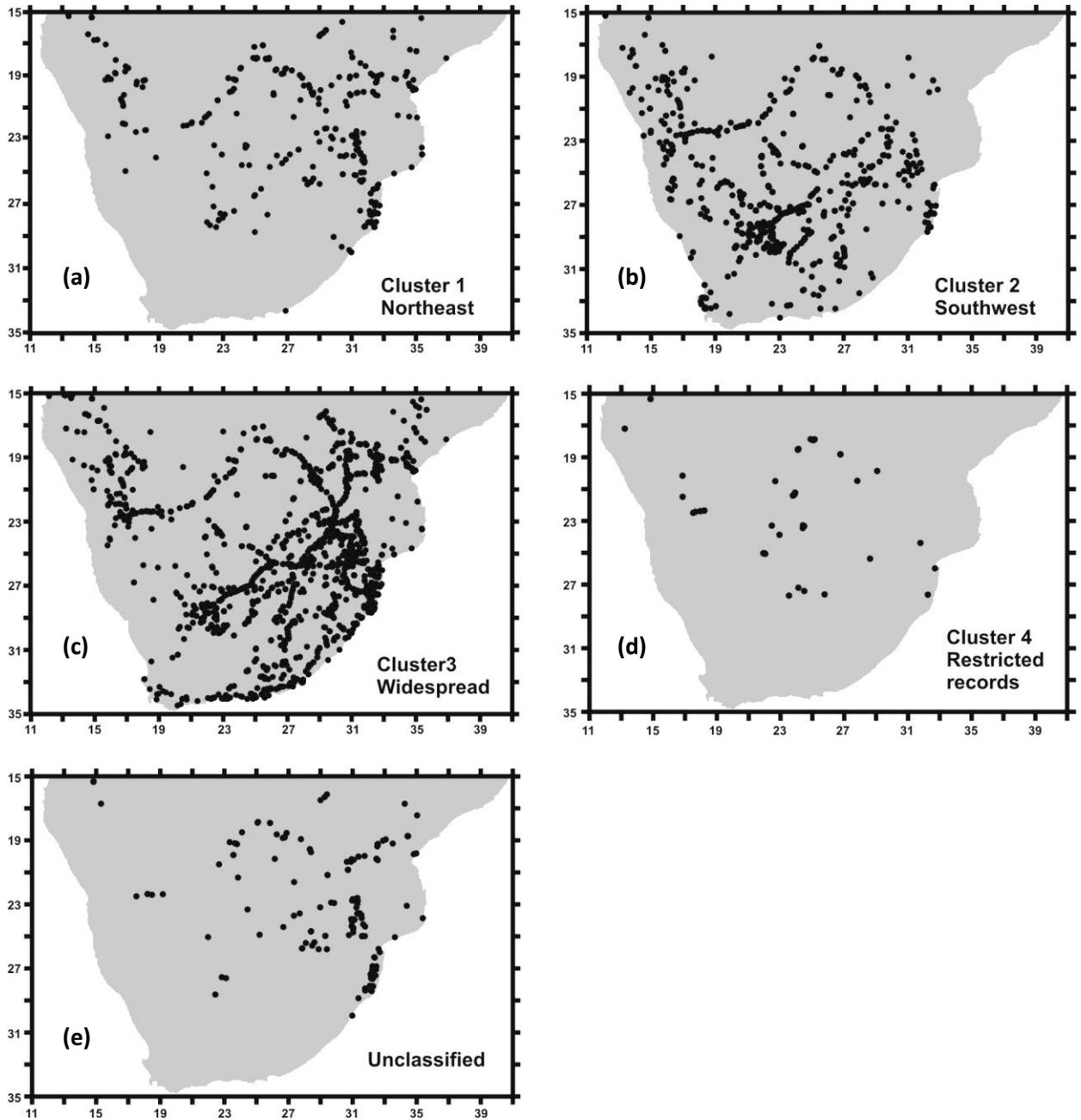


Figure 3.4. (a – e). Spot distribution for restricted/poorly recorded, unclassified and three biogeographical groups or sub groups of dung beetles defined in the ordination plot (see figure 3.2)

Table 3.3. Variation across bait types (carrion, pig, elephant, cattle and sheep dung) for proportional biogeographical composition (species clusters defined in Fig. 3.1.) at the six study areas in Botswana

Mean percentage abundance of five bait types \pm SD

Biogeographical area	Mid-summer rainfall			Arid late summer rainfall			Chi-square(χ^2)	P	r
	Chobe River	Savuti	NC-Kalahari	Khutse	Mabuasehube	SW-Kalahari			
Widespread/northeast	26.12 \pm 10.81	6.74 \pm 8.55	8.49 \pm 6.89	0.02 \pm 0.04	0.04 \pm 0.06	0.00	36.46	0.01	0.30
Widespread	32.36 \pm 4.56	13.33 \pm 7.28	10.41 \pm 8.47	39.05 \pm 20.58	1.09 \pm 0.80	0.62 \pm 0.21	37.62	0.01	0.24
Northeast - bias	24.35 \pm 8.18	42.33 \pm 18.88	3.54 \pm 3.80	0.97 \pm 0.55	0.06 \pm 0.07	0.00	11.83	0.92	0.15
Southwest - bias	17.11 \pm 6.52	37.35 \pm 15.68	77.39 \pm 10.14	59.25 \pm 20.08	98.56 \pm 0.78	99.38 \pm 0.21	62.02	0.00	0.18
Poorly recorded	0.05 \pm 0.04	0.25 \pm 0.25	0.16 \pm 0.19	0.72 \pm 0.64	0.26 \pm 0.47	0.00	0.41	1.00	0.05

3.4. Discussion

The present SW Kalahari region is considered to be the SW end of an arid corridor that connected NE and SW Africa in the glacial periods of the Pleistocene (Lamoral, 1978; 1979). This arid corridor has been recently cut by increasing rainfall in central Africa creating an aridity gradient from NE –SW in southern Africa.

As previously noted by Davis (1993, 1997), this climatic history has resulted in equivalently strong NE / SW patterns in the biogeography of dung beetles in southern Africa due to differences in both the periodicity and amounts of seasonal rainfall. Such distinct faunal differences between NE regions with higher mid-summer rainfall peaks and SW regions with lower late summer rainfall peaks are supported by the current results showing distinct differences in biogeographical composition between the more mesic NE savanna and the arid Kalahari in the SW.

Within Botswana, the increasing aridity to the SW has presumably acted as a filter for psammophilous NE moist savanna species with a limited tolerance of increasingly arid conditions leading to high species turnover (Chapter 4) between the moister NE and the NE/Kalahari transitional zones and their replacement by endemic Kalahari elements to the SW. This is also supported by the greater biogeographical diversity in the NE and severely limited diversity in the SW that is dominated in the extreme by SW biogeographical elements. Consequently the hypothesis of decreasing biogeographical diversity in the fauna and increasing endemism to the SW is supported. Although there is some variation in the proportional biogeographical composition on different bait types at each of the 6 study areas, there is no fundamental difference in biogeographical patterns across the aridity gradient on these different bait types.

The Kalahari deep sand may also constitute a barrier to some non-psammophilous invertebrates. Although no current data were recorded to determine the effect of the Kalahari deep sands on barring dung beetle species associated with finer-grained soils, there is evidence that the sand systems constitute barriers to non-psammophilous scorpions (Prendini, 2005). With regard to dung beetles, it is also likely that the Kalahari acts as a barrier to savanna species with such a habit. For example, *Onitis viridulus* is known to be widespread from southern to east Africa on finer-grained soils (A.L.V. Davis pers. comm.). However, in the present study, it was represented by only a single specimen recorded in the extreme NE on the deep sands of Chobe.

CHAPTER 4 PATTERNS OF SPECIES DIVERSITY, TURNOVER, AND FUNCTIONAL DIVERSITY ACROSS THE BOTSWANA KALAHARI

4.1. Introduction

Species diversity is influenced by historical, regional ecological and local ecological factors (Ricklefs & Schluter, 1993; Lobo & Davis, 1999). In Botswana, these include sand deposition and development of an aridity gradient (Cooke, 1985; Tyson, 1986), land system perturbations (De Wit & Bekker, 1990) and the frequency and density of available dung types (Tshikae *et al.*, 2008). For millennia these factors have interacted in ways that have influenced, respectively, species composition and species diversity in the region (Davis & Scholtz, 2004).

Species distribution patterns along environmental gradients have been extensively studied with different patterns of diversity and abundance always emerging. Studies in the USA and Brazil recorded an increase in species richness of gall-inducing insects with increase in elevation and aridity gradients (Fernandes and Price, 1988; Lara and Fernandes, 1996). However a study along the border between USA and Mexico, documented a decrease in both gall-inducing insects and tree species with increasing aridity (Blanche & Ludwig, 2001). Also in Australia there was no correlation between gall-inducing insect species richness and more arid environments (Blanche *et al.*, 2000). Recent studies in South Africa, at the Nama Karoo-Kalahari ecotone have also shown that dung beetle species richness declined along a gradient of increasing aridity, however decrease in diversity was associated with edaphic characteristics and drier conditions (Davis & Scholtz, 2004; Davis *et al.*, 2008). Also, functional composition varied along this aridity gradient with assemblages in the mesic NE comprising high proportions of tunnellers whereas those in the southwest were dominated by ball rollers (Davis & Scholtz, 2004).

In the above cited studies from South Africa, besides climatic considerations, variations in vegetative physiognomic and edaphic characteristics have influenced species distribution

patterns. The current study however was conducted in a region that provides a relatively homogeneous soil type (sand), but over a wide range of moisture regimes (Scholes *et al.*, 2004), with noticeable dung resource gradients (Chapter 2). In Chapter 3, it was found that the biogeographical patterns of scarabaeinae beetles were primarily influenced by climate variability and dung type at regional and local spatial scales respectively. There was variation in biogeographical composition between bait types in the NE and decreasing diversity in biogeographical composition along the NE–SW aridity gradient. The present chapter aims to examine patterns of species richness, alpha, beta, and functional diversity and the relative influence of the climatic gradients implied by differences between study areas and trophic factors. It was hypothesized that species richness will decline from NE to SW, possibly limited by increasingly less suitable climatic and ecological conditions, such as fewer rainfall events, fewer dung types, and lower vegetation heterogeneity.

4.2. Analytical Methods

4.2.1. Validity of data

Rarefaction curves and species estimator methods were used to assess the completeness of the species record for each study area. In each area, sample-based rarefaction was calculated from a matrix of species abundance by samples for each dung type using the EstimateS 7 computer package (Colwell, 2005). Average expected species richness was calculated using five different species estimators (Chao 1 & 2, Jackknife 1 & 2 and bootstrap). Proportional completeness of the species record was cited as a percentage of observed against estimated species richness.

4.2.2. Diversity indices

Alpha and Beta diversity (species turnover) for dung beetles were examined across the climatic gradient. The Shannon-Wiener index was used to measure alpha diversity on each bait type in each study area. This index is expressed as $H' = -\sum p_i \log_2 p_i$ where p_i represents the decimal proportion of the i th species. Whittaker's beta-diversity index is

considered one of the best early indices (Wilson & Schmida, 1984) for comparing species diversity between ecosystems or along environmental gradients. Hence it was selected for sequential pairwise comparison of study areas across the climatic gradient. It is expressed as Beta diversity, β_w :

$$\beta = \frac{S}{\bar{\alpha}} - 1$$

Where S = the total number of species recorded in both communities (study areas) and $\bar{\alpha}$ = the average number of species found within both communities along the environmental gradient.

4.2.3. Factors influencing species diversity

A GLM repeated measures ANOVA analysis was performed to determine the influence of spatial (6 study areas each with 3 study sites), trophic (5 bait types) and temporal factors (2x24 h sampling days) on total species richness, diversity, and abundance across the climatic gradient using Statistica, version 6.0 (Statsoft, 2008). Trap data on each sampling day were treated as repeated measures. Tukey's HSD post hoc tests were also conducted to determine which subjects are responsible for any significantly different variance that is detected.

4.2.4. Functional Diversity

The Kalahari basin dung beetle species were classified according to their behavioural patterns, comprising four principal functional groups defined by Doube (1990). The major functional groups comprise *ball-rollers* which roll a portion of dung away from the original dung pat before it is buried, *tunnellers* which provision tunnels made under the original dung pat with piece meal(dung balls), *kleptocoprids* which utilize dung buried by other dung beetles, and *endocoprids* which breed within the original dropping *in situ* (see Davis & Scholtz, 2001). In the present study, only the first 3 functional groups were recognized given that scarabaeinae endocoprids tend to be relatively uncommon compared to other

functional groups (see Doube, 1990; Davis, 1996c; Davis & Scholtz, 2001). This allowed for an assessment of the proportional representation of ball rollers, tunnellers, and kleptocoprids across the climatic gradient. For each study area the proportion of species in each functional group was expressed as a percentage of all species present in the study area.

4.2.5. Species abundance patterns

Dung beetle assemblages from the six study areas were compared using non-metric multidimensional scaling (MDS). Analyses were conducted on combined data for carrion and dung assemblages and on dung assemblages only. Ordination plots were used to display dung beetle assemblage relationships among the six study areas to reveal the differences in dung beetle community structure. In this case assemblages in areas or samples with higher similarity are placed closer to one another and the less similar assemblages are placed further apart.

Cluster analysis was used to both define dung beetle community divisions in relation to study areas across the climatic gradient and to support the ordination analysis. The same data were arranged as a matrix of mean species abundance per site per bait type. These data were fourth-root transformed before analysis and the nonmetric Bray-Curtis similarity coefficient was used to compute a similarity matrix. This matrix was subjected to the agglomerative clustering technique, group average linking, using the multivariate analytical computer package PRIMER Version 5.0 (Clarke & Warwick, 2001). Multiple paired comparisons of community clusters were conducted using ANOSIM, a subroutine of this package.

4.3. Results

4.3.1. Completeness of the species record

Almost all the rarefaction curves were near asymptote, suggesting that most species were sampled with each bait type (Fig. 4.1). Sampling of the study region can be considered representative as observed species richness of most bait types is greater than 70% of the predicted species. Furthermore predictions of local species richness for each bait type using 5 non-parametric estimators showed that species record was fairly complete (Table 4.1). Species richness was prominent in pig bait in all study areas except Savuti and Mabuasehube. Cattle dung bait lacked consistency across the study region while sheep bait attracted a high number of species in Mabuasehube and Sw-Kalahari. Carrion was lower everywhere except in north central Kalahari where it comes above some dung baits, perhaps due to opportunistic feeding of some species (see *Pachylomera femoralis*, Appendix A4).

4.3.2. Species richness, alpha and beta diversity patterns

A total of 123 497 individuals was trapped comprising 139 species. Both study areas and bait type had strong effects on diversity and species richness (Table 4.2). Chobe NP showed greater overall species richness and abundance than CKGR and KTP (Appendix A4). There was a decline in species numbers from Chobe then an increase at Khutse followed by decline (Appendix A4, Fig. 4.2). The same general pattern is shown by overall abundance and overall alpha diversity (Appendix A4). For detailed species richness, the above pattern is repeated in many cases (Table 4.3) with some exceptions (e.g. sheep & cattle to the SW). Detailed alpha diversity shows no such consistency in pattern (Table 4.4). Beta diversity patterns showed a peak in turnover between Savuti and NC-Kalahari followed by a decrease to the SW (Fig. 4.2).

Mean species numbers showed a decreasing trend from the mesic northeast to arid southwest (Fig. 4.2.). On the other hand pairwise turnovers (Beta diversity) in species composition across the environmental gradient were high between Savuti and NC-Kalahari

and also between NC-Kalahari and Khutse (Fig. 4.2). Intermediate beta diversity values were recorded between sites in Chobe River and Savuti and as well as between sites located in Khutse and Mabuasehube (Fig. 4.2). The dendrogram shows that Chobe River and Savuti assemblages grouped together separately from the Central and Southwest Kalahari assemblages (Fig. 4.3). Within the central-southwest Kalahari cluster, NC-Kalahari and Khutse were outliers to Mabuasehube and SW-Kalahari group, suggesting that though very similar and distinct from Chobe–Savuti assemblages, are nonetheless different from one another

4.3.3. Factors influencing diversity, abundance and species richness

Diversity, abundance and species richness were significantly different between study areas and bait type (Table 4.2). Tukey's HSD test showed significant differences in diversity between study areas with no clear regional patterns. However differences in bait types were primarily between dung and carrion baits (Table 4.4). In species richness, significant differences among study areas were mainly between NC-Kalahari and all study areas and also between SW-Kalahari and all study areas ($P < 0.05$). For bait types, post hoc tests showed that species richness differed significantly between carrion, omnivore, non-ruminant herbivore and ruminant baits ($P < 0.05$)(Table 4.4).

4.3.4. Species abundance patterns

The MDS ordination based on fourth-root transformation of a relative abundance matrix indicated carrion samples as scattered between assemblages from different study areas (Fig. 4.4a). A new analysis was performed with carrion samples removed and a new MDS plot with a lower stress value and distinct assemblages in each study area supported removal of carrion samples (Fig. 4.4b). Carrion samples were characterized by a few common species in particular *Scarabaeus flavicornis*, across the study region.

4.3.5. Cluster analysis results

Analysis of similarity (ANOSIM) indicates great variability in species composition between study areas (ANOSIM, Global R = 0.855, P < 0.01). Marked differences (ANOSIM, Global R = 1, P < 0.01) were found between study sites located in moister savanna (Chobe National Park) and arid Kalahari (Kgalagadi Transfrontier Park). Central Kalahari Game Reserve (CKGR) faunas were less similar (Figs 4.3 and 4.4b) than were Chobe NP and Kgalagadi Transfrontier Park (KTP) faunas suggesting more internal consistency between the faunas of Chobe NP and KTP than those within CKGR.

4.3.6. Functional patterns

Trends in functional group structure varied across the study region (Fig. 4.5). Kleptocoprids comprised the greatest proportion of dung beetles across the Kalahari basin. There was an increase in kleptocoprids from Chobe then a sharp decline at Khutse followed by an increase (Fig. 4.5). The proportion of ball rollers showed a decreasing trend from Chobe to NC-Kalahari that peaked sharply at Khutse and steadily decreased toward the arid SW while remaining proportionally higher than in the moister NE savanna. The proportion of tunnellers increased from Chobe to Savuti then steadily declined to Mabuasehube followed by slight increase to the arid SW-Kalahari (Fig. 4.5).

Table 4.1. (a) Observed species richness. (b) Mean estimated richness from 5 non-parametric estimators (Chao 1 & 2, Jackknife 1 & 2 and Bootstrap. (c) Percentage of estimated richness in five bait types across six study areas

	Observed richness					
	Chobe River	Savuti	NC-Kalahari	Khutse	Mabuasehube	SW-Kalahari
(a)						
Carrion	33	25	14	28	19	14
Pig	53	45	32	51	32	31
Elephant	47	50	27	47	28	23
Cattle	35	49	19	25	21	29
Sheep	52	35	12	22	38	31

Mean (\pm SD) estimated richness from five nonparametric estimators						
	Chobe River	Savuti	NC-Kalahari	Khutse	Mabuasehube	SW-Kalahari
(b)						
Carrion	40.3 (3.3)	34.3 (4.3)	20.2 (2.6)	28.6 (1.1)	19.2 (0.9)	16.9 (1.2)
Pig	77.0 (16.4)	55.5 (6.1)	60.5 (20.7)	61.4 (3.8)	39.0 (4.0)	31.7 (0.9)
Elephant	61.2 (11.1)	63.5 (5.9)	35.0 (3.5)	52.9 (2.1)	31.5 (1.2)	26.1 (1.1)
Cattle	40.2 (4.2)	57.6 (4.0)	26.0 (3.6)	28.5 (1.6)	28.9 (4.7)	32.2 (1.2)
Sheep	93.5 (36.1)	39.4 (1.4)	16.5 (2.2)	27.7 (2.1)	63.7 (19.3)	41.5 (6.7)
Percentage of estimated species richness						
	Chobe River	Savuti	NC-Kalahari	Khutse	Mabuasehube	SW-Kalahari
(c)						
Carrion	81.89	72.89	69.31	97.90	98.96	82.84
Pig	68.83	81.08	52.89	83.06	82.05	97.79
Elephant	76.80	78.74	77.14	88.85	88.89	88.12
Cattle	87.06	85.07	73.08	87.72	72.66	90.06
Sheep	55.61	88.83	72.73	79.42	59.65	74.70

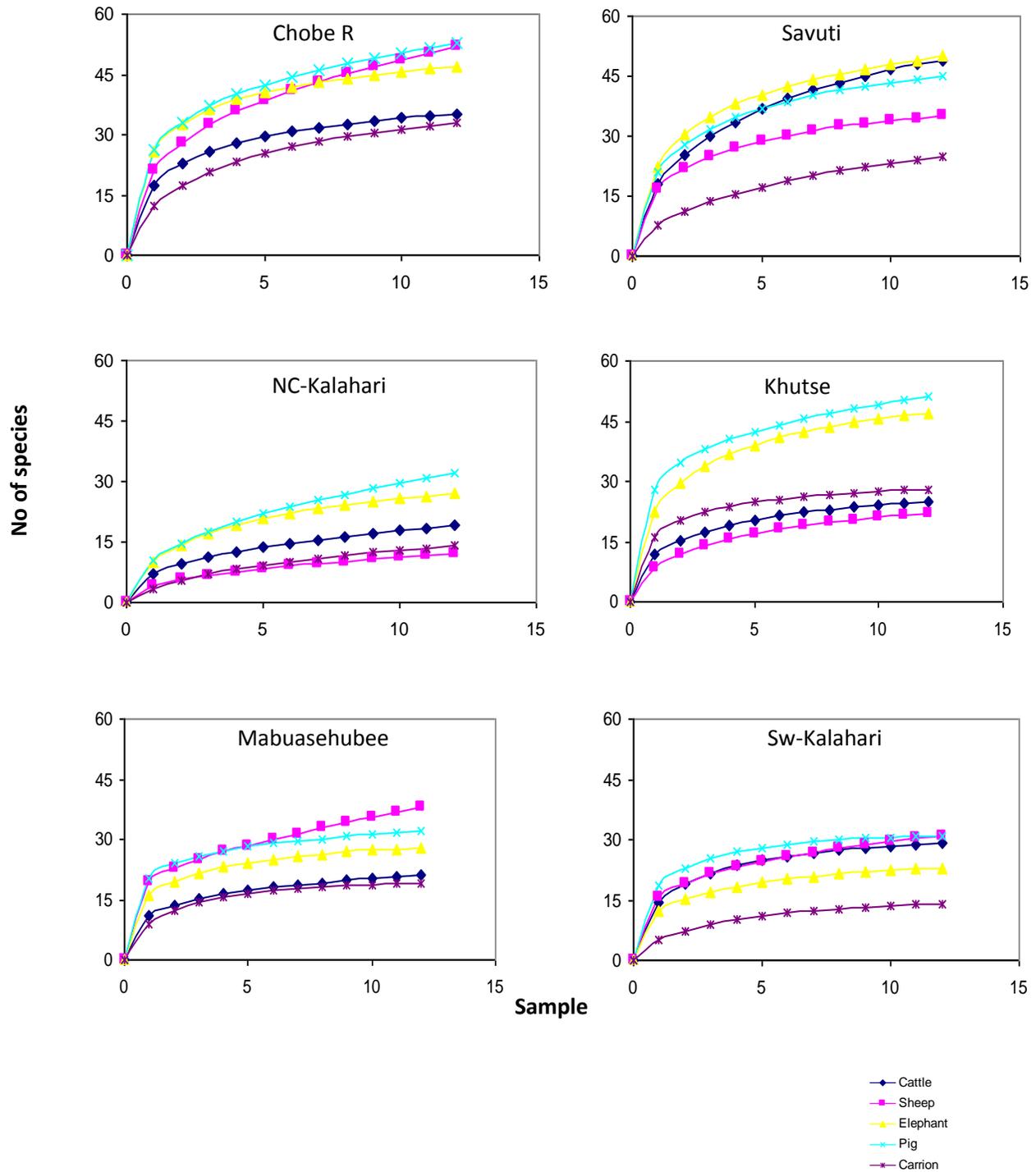


Figure 4.1. Sample based rarefaction curves for species on five different bait types in all six study areas

Table 4.2. Results for a General Linear Model (GLM) of factors influencing diversity, species richness and abundance of dung beetles across the Kalahari in Botswana

	F - value	DF	P- value
Diversity (Shannon-Wiener)			
Place (Study area)	71.81	5	***
Bait type	33.80	4	***
Place * Bait type	11.17	20	***
Day	0.38	1	NS
Day * Place	11.89	5	***
Day * Bait type	1.05	4	NS
Day * Place * Bait type	2.68	20	***
Observed species (S)			
Place (Study area)	65.00	5	***
Bait type	91.26	4	***
Place * Bait type	11.39	20	***
Day	0.74	1	NS
Day * Place	16.46	5	***
Day * Bait type	1.44	4	NS
Day * Place * Bait type	5.35	20	***
Abundance (N)			
Place (Study area)	24.29	5	***
Bait type	49.16	4	***
Place * Bait type	7.89	20	***
Day	0.02	1	NS
Day * Place	1.86	5	NS
Day * Bait type	0.26	4	NS
Day * Place * Bait type	1.04	20	NS

*** $P < 0.001$; NS, not significant

Table 4.3. Distribution of mean diversity and species richness of dung beetles in five bait types across the Kalahari in Botswana

	Carrion	Pig	Elephant	Cattle	sheep
Mean diversity / trap ± S.D.					
Chobe River	1.45 ± 0.69 ^{de}	1.46 ± 0.65 ^{ab}	1.57 ± 0.85 ^{bc}	1.82 ± 0.53 ^{bc}	1.83 ± 0.67 ^a
Savuti	1.29 ± 0.30 ^{ce}	1.90 ± 0.13 ^{cd}	1.98 ± 0.30 ^{ac}	1.99 ± 0.37 ^b	2.07 ± 0.30 ^a
NC-Kalahari	0.52 ± 0.41 ^a	1.12 ± 0.43 ^a	1.29 ± 0.34 ^b	1.04 ± 0.30 ^a	0.65 ± 0.52 ^b
Khutse	1.90 ± 0.30 ^{bd}	1.89 ± 0.64 ^{cd}	2.07 ± 0.25 ^{ac}	1.69 ± 0.32 ^{b^c}	0.95 ± 0.47 ^b
Mabuasehube	1.22 ± 0.43 ^{ef}	1.98 ± 0.22 ^c	1.85 ± 0.17 ^c	1.66 ± 0.24 ^c	2.08 ± 0.15 ^a
Sw-Kalahari	0.89 ± 0.37 ^{af}	1.60 ± 0.46 ^{bd}	1.53 ± 0.26 ^{bc}	1.75 ± 0.24 ^{bc}	1.93 ± 0.27 ^a
One-way ANOVA results	F _(5, 138) = 35.52***	F _(5, 138) = 17.95***	F _(5, 138) = 9.56***	F _(5, 138) = 16.59***	F _(5, 138) = 34.97***
Mean species richness / trap ± S.D.					
Chobe River	7.38 ± 4.80 ^c	18.00 ± 8.86 ^{bc}	15.04 ± 11.21 ^c	12.38 ± 5.62 ^b	15.42 ± 8.18 ^b
Savuti	5.67 ± 2.06 ^{cd}	16.08 ± 4.83 ^c	15.54 ± 4.92 ^c	13.38 ± 5.11 ^b	13.17 ± 4.22 ^b
NC-Kalahari	2.33 ± 1.13 ^{bd}	7.33 ± 3.31 ^a	7.42 ± 2.41 ^a	5.13 ± 1.48 ^a	2.75 ± 1.54 ^a
Khutse	12.71 ± 4.44 ^a	22.21 ± 7.97 ^b	16.38 ± 5.74 ^c	8.54 ± 2.64 ^c	5.83 ± 2.08 ^a
Mabuasehube	5.75 ± 1.75 ^{cd}	16.33 ± 2.06 ^c	12.71 ± 2.20 ^{bc}	8.50 ± 2.30 ^c	15.63 ± 4.11 ^b
Sw-Kalahari	3.46 ± 1.67 ^d	13.88 ± 3.79 ^c	9.33 ± 2.51 ^{ab}	10.88 ± 2.69 ^{bc}	12.83 ± 3.17 ^b
One-way ANOVA results	F _(5, 138) = 23.04***	F _(5, 138) = 12.19***	F _(5, 138) = 9.04***	F _(5, 138) = 20.21***	F _(5, 138) = 40.95***

*P < 0.05; **P < 0.001; ***P < 0.0001. In each column; values followed by a different letter differed significantly (Tukey's HSD).

Table 4.4. Overall mean diversity and species richness in all bait types and across study areas

Bait type	Overall (H')	Overall(spp)
Carrion	1.20 ± 0.62 ^a	6.22 ± 4.46 ^a
Pig	1.66 ± 0.55 ^b	15.64 ± 7.19 ^b
Elephant	1.70 ± 0.52 ^b	12.74 ± 6.58 ^c
Cattle	1.65 ± 0.45 ^b	9.80 ± 4.52 ^d
Sheep	1.57 ± 0.72 ^b	10.94 ± 6.57 ^d
Places		
Chobe River	1.63 ± 0.11 ^{bd}	13.64 ± 2.58 ^b
Savuti	1.85 ± 0.09 ^c	12.77 ± 1.26 ^{bc}
NC-Kalahari	0.92 ± 0.09 ^a	4.99 ± 0.88 ^a
Khutse	1.67 ± 0.11 ^{bd}	13.13 ± 2.39 ^{bc}
Mabuasehube	1.74 ± 0.13 ^{bc}	11.78 ± 0.93 ^{cc}
Sw-Kalahari	1.53 ± 0.10 ^d	10.08 ± 0.79 ^d

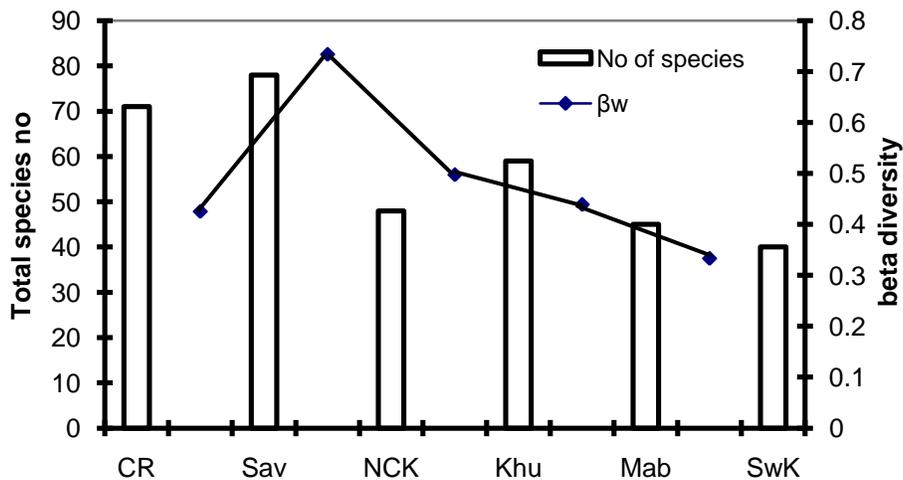


Figure 4.2. Observed total number of species and pairwise turnover in species composition between study areas along an aridity gradient. (CR) Chobe River; (Sav) Savuti; (NCK) North Central Kalahari; (Khu) Khutse; (Mab) Mabuasehube; (SwK)- Southwest Kalahari

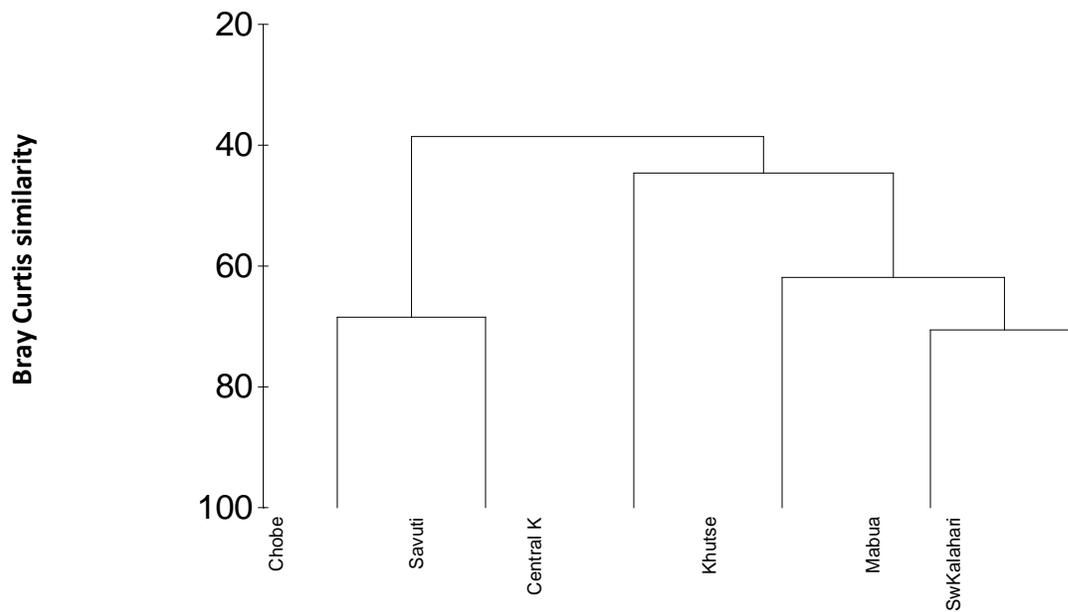


Figure 4.3. Dendrogram showing percentage similarity between dung beetle assemblages along the aridity gradient in the Botswana Kalahari (Central-K: North Central Kalahari; Mabua: Mabuasehube; Sw-K: Southwest Kalahari)

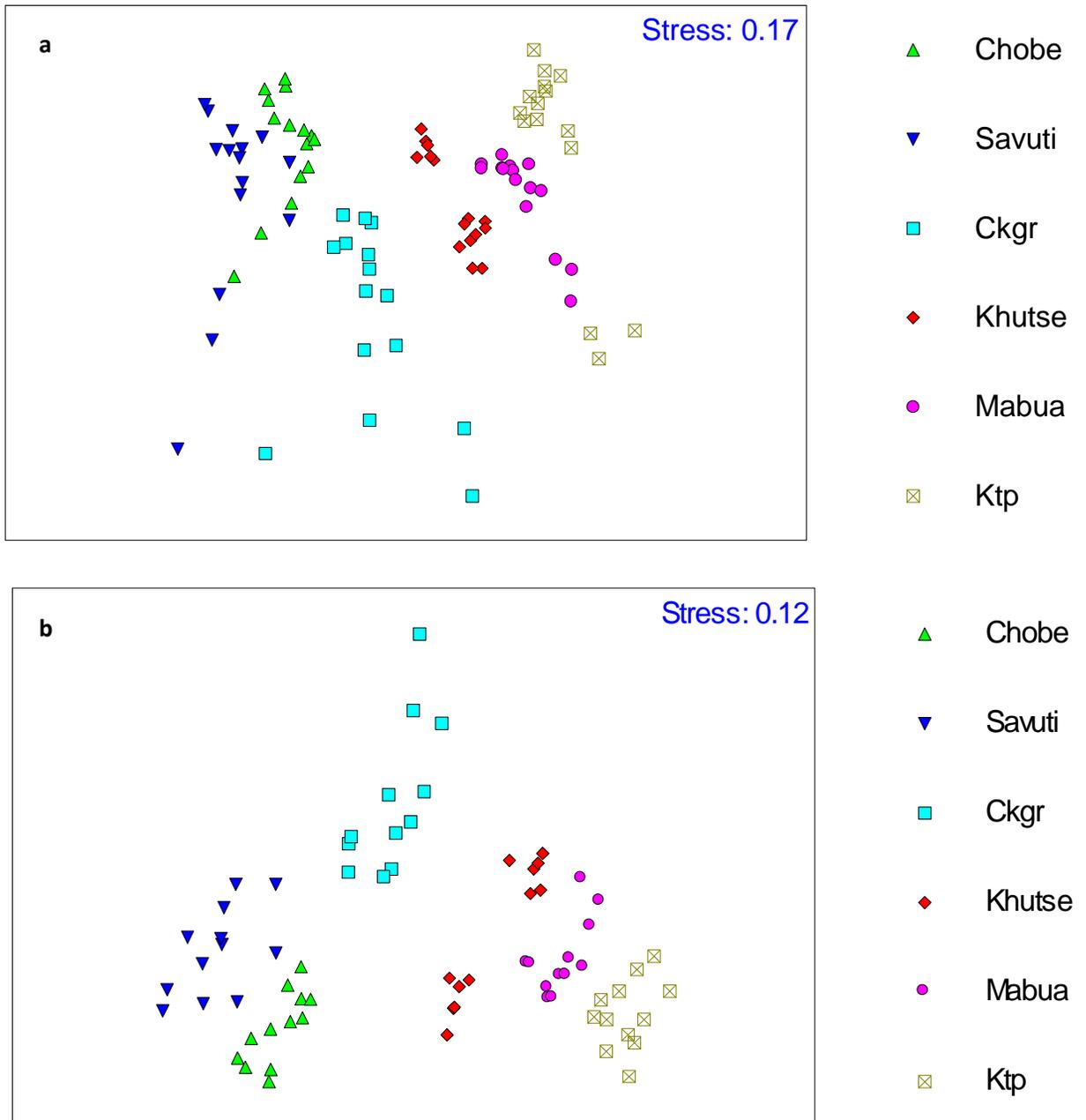


Figure 4.4. Non-metric Multidimensional Scaling (MDS) ordination of species abundance for dung beetles trapped to (a) dung and carrion baits and (b) dung baits only, in six study areas.

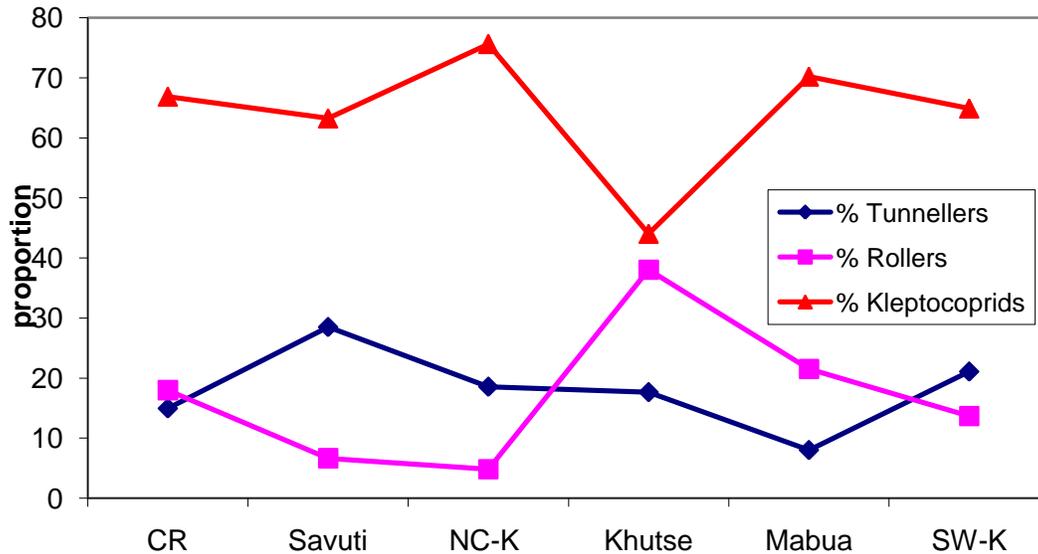


Figure 4.5. Proportion of the three common functional groups in six study areas (see Fig 4.3 for key of study areas).

4.4. Discussion

It is widely known that the Kalahari basin is characterized by climatic and physiognomic variability from the mesic northeast to the arid southwest (Davis, 1987; Davis, 1997; Cowling *et al.*, 2003). This gradual change in the climate and vegetation has greatly influenced the distribution of the grasshopper (Barker, 1993) and herpetofauna (Haacke, 1984). Dung beetles are by no means an exception (Davis & Scholtz, 2004). Several studies have demonstrated that environmental gradients and ecological changes involving quantity and quality of dung types produce changes in species composition, abundance and other attributes, including functional diversity (Lumaret *et al.*, 1992; Davis, 1994a; Carpaneto, 2005).

The results of this study show patterns of dung beetle assemblage structure that could be linked to the influence of the aridity gradient and perhaps mammal diversity. This was

demonstrated by the great overall species richness, abundance, high turnover and differences in community patterns between the six study areas. It was also exemplified by the greater overall abundance and species richness in sites located at Chobe River and Savuti where there is higher rainfall and a full range of dung types. While both attributes plummeted at NC-Kalahari before slightly peaking at Khutse and then levelling off towards the SW-Kalahari sites where a single dung type (pellets), in particular, dominates. The fact that overall species richness and abundance in NC-Kalahari were lower than in Khutse could imply that the local environmental conditions (habitat heterogeneity) between these two areas are different, as highlighted by a higher concentration of pans in NC-Kalahari than in Khutse. Apart from habitat heterogeneity it appears that mammals in these two areas also utilized habitats differently. Throughout the study, animal herds in NC-Kalahari were mostly seen on the pan and pan edges. This may have been to avoid long grass in sandy habitats in order to have a clear view of predators. While in Khutse animal herds, in particular gemsbok (*Oryx gazella*), were mostly seen on sandy habitats where the grass was short and predators could be seen from a distance. Thus, the relatively low averages of dung beetles in NC-Kalahari most likely reflect differences in mammal and therefore dung density between places.

Despite the relatively species rich dung beetle communities within the Kalahari basin, community composition varies greatly over several scales, with an exceptionally high (c. 0.73) species turnover (Beta-diversity) between some study areas along the aridity gradient. This high species turnover, especially between Savuti and NC-Kalahari, would be due to species lost through lower species richness in NC-Kalahari. It may also be consistent with the abrupt changes in climate and vegetation physiognomic features as well as changes in dung types. However, more interesting is the beta diversity between NC-Kalahari and Khutse. Turnover between NC-Kalahari and Khutse perhaps demonstrates differences in local environmental conditions rather than vegetation and dung type which remain similar in these two localities. NC-Kalahari is at the edge of the Makgadikgadi depression and has a high concentration of pans with patches of deep sand stretching 3-4 Km between them. Possibly the species area relationships effect (Gaston & Lawton, 1990) due to smaller and fewer sand pockets as compared to extensive pans. In addition it could mean that Khutse is

drier than NC-Kalahari, being a transitional zone to proper Kalahari, lying within the 350 mm isohyet. The presence of *Pachylomera opacus* and *Scarabaeus proboscideus*, arid specialists, in Khutse gives emphasis to this claim (see Davis, 1997). Furthermore, the high turnover values possibly indicate the proximity of cattle posts to the Khutse Game Reserve boundary hence to sampling sites (approximately, 17 Km) which perhaps locate them within the flight ranges of such large ball rollers as *P. femoralis* and *Kheper lamarcki* which were present and more abundant in Khutse while absent in NC-Kalahari. These are likely to be supported by copious amount of domestic animal dung especially cattle and horse.

In this study, a clear trend in the proportion of functional groups especially in the roller taxa occurs between the moister and arid areas. Ball rollers are proportionally more abundant in the arid Kalahari than in the moister savanna. However, tunnellers were also found to be proportionally more abundant than rollers in the SW-Kalahari, a habitat that is dominated by pellet dung. This proportional pattern, particularly in ball rollers is also observed in the Kalahari / Nama-Karoo ecotone, where there are climate and habitat gradients (Davis & Scholtz, 2004; Davis *et al.*, 2008). Ball rollers were proportionally higher in the Nama-Karoo which is hyper-arid and characterized by stony Karoo sands than in the much moister Kalahari deep sands. In another study carried out in South Africa under similar rainfall conditions proportions of ball rollers increased from clay to sandy habitats in Gauteng and the reverse in Mkuze (Davis, 1996c). In above studies it is clear that functional group structure responds to habitat differences (Davis, 1996c; Davis & Scholtz, 2004). However, proportional functional groups showed no consistent relationship with any particular habitat type.