Edaphic and climatic history has driven current dung beetle species pool and assemblage structure across a transition zone in central South Africa

ADRIAN L.V. DAVIS, CLARKE H. SCHOLTZ, CHRISTIAN M. DESCHODT and WERNER P. STRÜMPHER

Scarab Research Group, Dept of Zoology and Entomology, University of Pretoria, Private Bag X20, Hatfield, 0028 South Africa

Running head: Historically-based drivers of dung beetle assemblages

Dr Adrian L.V. Davis

Scarab Research Group

Department of Zoology & Entomology

University of Pretoria

Private Bag X20

Hatfield

0028 South Africa

e-mail: adavis@zoology.up.ac.za

Tel. 0027 12 420 2539 (landline)

Tel. 0027 78 175 8441 (mobile)

ABSTRACT

We investigate biogeographical, regional and sub-regional scale responses of scarabaeine dung beetles to late Cenozoic changes in edaphic and climatic character that created a Savanna / Karoo transition zone in the Northern Cape, South Africa. Across a 50,200 km^2 study area, the Northern Cape species pool comprised six biogeographical groups defined from distribution across Southern Africa. These species groups contributed in different proportions to five regional assemblages defined from structural differences across the transition zone. Towards transition zone peripheries, regional assemblage structure was more strongly correlated to sandiness dating from Miocene to Pliocene deposition (Kalahari), aridity dating from Pliocene to Pleistocene climatic change (Bushmanland Karoo), or cooler temperatures dating from Miocene to Pliocene uplift (Upper Karoo). Correlates of sub-regional assemblages trended to intensification of dominant drivers towards regional peripheries. Drivers of central transition zone, regional assemblages ("Gariep Karoo", "Gariep Stony Karoo") showed no dominance. Biogeographically, endemism dominates the Northern Cape transition zone: southwest arid groups in Nama Karoo regions; Kalahari plus northeast savanna groups in the Kalahari. Regionally, transition drives assemblage structure: unique variance, 60% in the Kalahari, 21-30% in four Nama Karoo regions; shared variance (overlap), 25-65% between Kalahari and warmer Karoo regions, 11-71% between mainly cooler Karoo regions.

ADDITIONAL KEYWORDS: Miocene – Pliocene – Scarabaeinae – structural drivers

INTRODUCTION

Changes in numbers of species and assemblage composition across geographical transitions reflect the traits of the available pool of species and their selective suitability across gradients of functional ecological factors that have developed over an evolutionary timescale (Carnicer *et al*., 2012). Current selection across transitions in terrestrial situations may be variously driven by biotic ecological factors such as productivity or vegetation structure (Hawkins *et al*., 2003; Arnan *et al*., 2014) that result from interaction between abiotic environmental drivers such as climate (temperature / rainfall) (Carnicer & Díaz-Delgado, 2008; Hawkins *et al*., 2003), topography (Davis *et al*., 1999; Hodkinson, 2005) or edaphic character (Tuomisto *et al*., 2014). Topography, landscape and vegetation heterogeneity have received much attention as drivers of variation in species numbers and assemblage composition whereas few studies have concentrated on climatic and edaphic drivers (Stein & Kreft, 2015). A previous study across the complex macroclimatic and edaphic Savanna / Nama Karoo transition zone in the Northern Cape, South Africa (Davis *et al*., 2008), has shown how dung beetle responses to edaphic and climatic factors interact at several different spatial scales to drive regional differences in species assemblages. The present study expands upon these findings using a geographically and faunistically more extensive data set, which is placed in an historical context.

In the Northern Cape transition zone, the main historical influences on the current species pool and regional assemblages may be dated to Miocene / Pliocene uplift in the southeast (Upper Karoo and Highveld; collectively the Drakensberg uplift zone), leading to erosion and sand deposition in the northwest (Kalahari Basin), followed by Pliocene / Pleistocene aridification that was most intense in the southwest (Bushmanland) (Dauteuil *et al*., 2015). In particular, the probable late Cretaceous down-warping in the centre of the Southern African subcontinent created the Kalahari Sag Basin into which sediments that now form the Kalahari Group strata were deposited under moist climate (Haddon & McCarthy, 2005). The subsequent late Miocene and Pliocene uplift along the southeastern edge of the basin created the cooler uplands of the Highveld and Upper Karoo from which rivers drained into the basin. This resulted in riverine erosion of exposed sandstone and deposition of sand over the earlier Kalahari strata (Haddon & McCarthy, 2005). In places, the sand was reworked into dunes by Pleistocene aeolian processes, especially during cooler, drier climatic phases (Stokes *et al*., 1998). Over the same late Cenozoic period, Pliocene intensification of polar glaciation (McKay *et al*., 2012)

and intensification of the cold Benguela upwelling on the southwest coast of Africa (Marlow *et al.*, 2000) caused the seasonal northeast shift of the westerly cell of wind currents lying over the South Atlantic Ocean to create the winter rainfall region in the Western Cape (Deacon, 1983). Thereafter, this area transitioned into the displaced summer rainfall region across an arid zone, which is most intense in the southwest of the study area where Bushmanland now comprises a mid-Miocene erosion surface comprising poorly preserved branching rivers on a low-lying plain (de Wit & Bamford, 1993). At the present time, there is seasonal oscillation in the expansion and contraction of the westerly and easterly cells of wind currents, the latter centred over the Indian Ocean (Tyson, 1986). This means that, on average, the southwest expansion of the easterly winds only reach the Northern Cape in late summer. Hence the increasing aridity from the Kalahari into Bushmanland southwestwards across the late summer rainfall region. Such climatic evolution favours a localized, arid-adapted species pool. This is partly supported by Davis (1997) who demonstrated areas of endemism centred on both the southwest Kalahari and the arid late summer rainfall region.

Species pools may be defined in different ways. Carstensen *et al.* (2013) identified various former approaches related to data usage and proposed several methods to standardize the definition of what they termed "the biogeographic species pool". This comprised a top down subdivision of large-scale distribution data to determine biogeographical regions with their objectively defined constituent species pools. However, the present study employs the bottom up method used to compare regional and local species numbers (Ricklefs, 1987; Lobo & Davis, 1999). Thus, a regional species pool was constructed from a collection of local species records. Species pools defined in such a manner are considered somewhat arbitrary (Carstensen *et al.*, 2013) as they emanate from an often subjectively defined geographical area. However, the present species pool recorded within the study area in the Northern Cape is placed in context by investigations into the relative influence of the different biogeographical regions found on the surrounding subcontinent.

In fossorial insect assemblages such as dung beetles, regional-scale community structure varies in species composition and relative abundance according to edaphic and macroclimatic factors (Tshikae *et al.*, 2013a). Therefore, historical development of north-south trends in soils and east-west gradients in rainfall / temperature have strongly influenced current regional and local functional ecological responses across the Northern Cape transition zone (Davis *et al.*, 2008). Surface microclimate may also be a major determinant of dung beetle assemblage structure as modified by vegetative structure (Davis *et al.*, 2013) although, presumably, this would be of limited importance in the arid Northern Cape owing to the largely sparse and open surface cover that provides little shade. It may be noteworthy that regional classification of dung beetle assemblage structure across the transition zone parallels biome-scale floral classification but diverges at bioregion scale (Davis *et al.*, 2008).

Previous work on the role of species traits in rules of species assembly identified body size and competition as major structural influences in some insect communities (Gotelli & Ellison, 2002; Fayle *et al.*, 2015). Such rules would be expected to also apply to dung beetle assemblages, which comprise a competitive hierarchy (Hanski & Cambefort, 1991) that is divisible into seven functional groups (Doube, 1990) based on combinations from an array of different body sizes from 1->2 000 mg dry weight and four principal behavioural types as regards sequestration of dung and its dispersal in space. These behavioural types comprise rolling balls of dung away from a dropping (telecoprids or ball rollers), burying it in tunnels excavated from under the dung (paracoprids or tunnelers), using dung buried by other scarabaeine beetles (kleptocoprids), or using droppings in situ (endocoprids) (Bornemissza, 1969). In the case of Northern Cape dung beetle assemblages, it is suggested that they would be structured by various functional biotic factors. These would include the relative suitability of different types of dung exploitation behaviour to dung pellets, which would dominate available dung types in the arid Northern Cape as supported by the trend from mesic to low-productivity arid climates in neighbouring Botswana where there is a decline and loss of large mammals dropping large dung types and an increase in those dropping pellets (Tshikae *et al.*, 2013b). Other factors would be separation across time by different diel activity patterns and limits on ecological similarity through body size and dung exploitation behaviour hierarchies, which may promote reduction or avoidance of competition.

The principal aims were to examine how geological and climatic history of the Southern African subcontinent has influenced current ecological setting in the Northern Cape transition zone. (1) Biogeographical groups were defined from the Northern Cape species pool using an improved distributional database for dung beetles. This database was used to plot and analyze distribution across the climate types of Southern Africa south of 15°S. (2) Regions and sub-regions were defined for the enlarged Northern Cape study area from structural analysis of 412 species data sets. (3) Proportional biogeographical group composition was determined for each Northern Cape region. (4) Relative influence of potential abiotic drivers was determined for each region and sub-region from correlations between faunal data and environmental factors. (5) Proportional functional structure was defined for dung beetle assemblages of each Northern Cape region using a body size and behavioural classification. (6) Northern Cape regions defined for dung beetles were compared with those defined for flora by Mucina & Rutherford (2006).

METHODS

SOUTHERN AFRICA AND NORTHERN CAPE

The Southern African subcontinent is fringed by a mostly narrow band of coastal lowlands almost entirely bordered by mountain escarpments that delineate a slightly tilted plateau with its lowest points in the western interior and greatest heights in the east (Partridge & Maud, 1987; Maud, 2012). A southwest / northeast climatic trend (Walter & Lieth, 1964) overlies this geomorphology and is roughly coincidental with principal floral biomes as defined by Mucina & Rutherford (2006) for South Africa. The southwest and southeast comprise winter or bimodal spring / autumn climate that support the Fynbos or Albany Thicket Biomes in moister areas. These merge into arid areas that support Succulent Karoo in the more winter rainfall-influenced southwest and Nama Karoo in the more late summer rainfall-influenced northeast. Further northeast, the moist, mid-summer rainfall climate supports the Indian Ocean Coastal Biome on the east coast; the Grassland Biome in higher altitude, southeast areas; and the Savanna Biome in the remaining areas.

The study area of 50,200 km^2 in the Northern Cape, South Africa, is bisected by the Orange River Valley at the point where it forms the boundary between the Savanna (SV) and Nama Karoo (NK) Biomes (Fig. 1) in the arid late summer rainfall region (Fig. 2). The area covers parts of four floral bioregions (Mucina & Rutherford, 2006). Two comprise the arid Kalahari Duneveld (SVkd - 51 study sites) and dry Eastern Kalahari Bushveld (SVk - 45 study sites), which lay to the northwest and northeast and are dominated by deep sands. The other two comprise the arid Bushmanland & West Griqualand (NKb - 167 study sites) and cooler, dry, Upper Karoo (NKu - 136 study sites), which lay to the southwest and southeast and are dominated by finer-grained soils with scattered, mostly sandy pans. Each bioregion comprised a number of vegetation units. The distribution of study sites between these units is described in Table S1.

NORTHERN CAPE SAMPLING

Dung beetle assemblage structure (species and their abundances) were determined at 400 study sites on 87 farms and six sites in Tswalu Kalahari Reserve (Fig.1) on single sampling occasions. Study sites were mostly >1 km apart and not closer than 450 m. Total data sets amounted to 412 since data were recorded at six of the study sites on two separate occasions, one after substantial rainfall and one during drought (Farm Brulpan (1)). Data were amassed over a period of 10 years from 2001 till 2011 with a hiatus in 2002. Data were recorded from 1-12 farms per year (Table S2) and from 1-3 farms per sampling occasion. As peaks in average rainfall occur during late summer across the study area (Walter & Lieth, 1964), data were recorded primarily during March each year, except for a few sites studied in late February or early April. Sites were selected to sample from main habitat types on each farm.

At each study site, dung beetle assemblages were sampled using three pitfall traps (2 L buckets) at 10 m intervals, each baited with a *circa* 250 ml composite of cattle and sheep dung (50/50), which are the principal farm livestock in the study area. Each bait was wrapped in thin cloth to exclude beetles, deep frozen and, then, defrosted before use when it was supported at ground level above a trap using two strong wires. At each site,
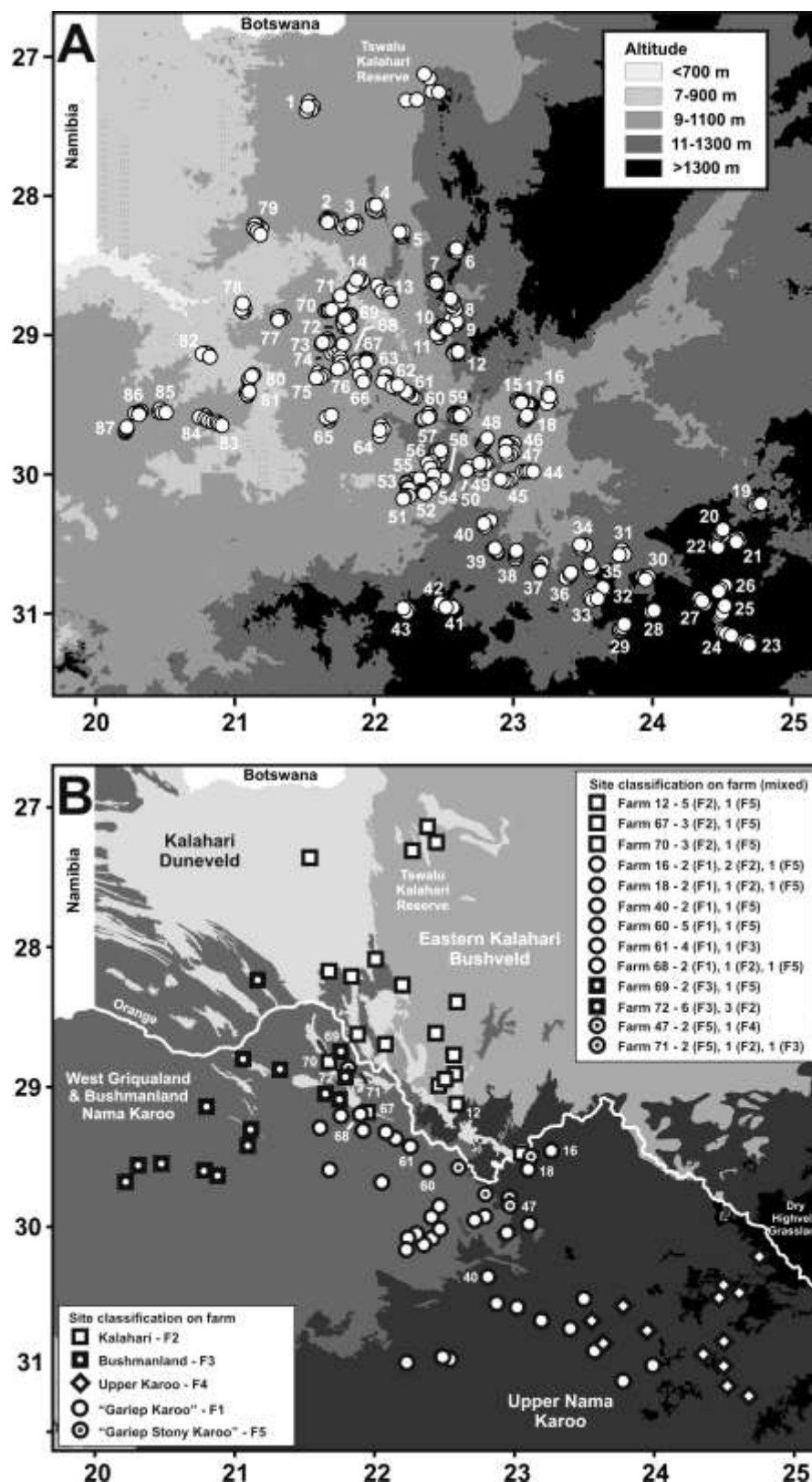
Figure 1. The Northern Cape study area, South Africa. A. Location of 412 study sites on 87 farms and one private reserve (key to farms: Table S2). B. Regional classification of 87 farms (single data points) and one private reserve (three data points) (See Fig. 3) plotted on a basemap of floral bioregions (Mucina & Rutherford, 2006).

sampling was conducted over 48 h. Traps were rebaited every 12 h so that fresh dung was presented to both diurnal and night-flying taxa. The catch was removed to storage in 70% alcohol after each 24 h period. Representative reference material is deposited at the University of Pretoria.

NORTHERN CAPE ENVIRONMENT

Environmental data were measured in the field or extracted from maps. Spot altitude at study sites was measured by GPS. GIS base maps were used to extract annual rainfall (1x1 km^2 polygons), annual temperature (max. + min. / 2) (5x5 km^2 polygons) and proportional contribution of sand grains to soils (FAO, 2012 - USDA soil classification). In some cases, classification of soil type was adjusted using on-site observations since the soil map was not always accurate at local scale. Classification of deep versus stony soils was also made by on-site observations.

DATA ANALYSIS
SPECIES POOL AND BIOGEOGRAPHY

The total number of dung beetle taxa recorded by sampling within the Northern Cape study area was defined as the species pool. Groups of species with differing biogeographical distribution patterns were determined by analyzing their wider occurrence across the climatic regions of Southern Africa south of 15°S as defined by Walter & Lieth (1964). This classification divides southern Africa into 26 climate types comprising variants of mediterranean-type winter rainfall (IV), bimodal spring / autumn rainfall (V) or arid climate (III) in the southwest and moist, warm temperate, summer rainfall climate (II) in the northeast. Climatic distribution data were determined for 113 out of 127 recorded species using an unpublished database (Table S1). Distributions of these species were quantified by plotting their occurrences on a GIS basemap and counting the number of degree squares occupied in each of the 26 climate types. As numbers of observations varied between species, data were standardized by conversion to proportions on a 0-1 scale for each species. The data matrix of 113 species by proportional occurrence in each of 26 climate types was analyzed by hierarchical factor analysis using principal components to extract an optimum of six factors (Statsoft, 2015 - Statistica v.12). Varimax normalized rotation was used to maximize patterns of high loadings along factors for clusters of species with similar biogeographical patterns. The matrix of correlations between oblique factors was subjected to a second factor analysis to extract extended factors representing shared (S factors) or unique variance (P factors). Coefficients of determination (r^2) derived from correlations between oblique and orthogonal extended factors show the proportion of shared and unique variance within clusters.

NORTHERN CAPE REGIONS

Northern Cape study sites with similar species assemblage structure were classified into regions using ordination (Statsoft, 2015 - Statistica v.12). A data matrix was constructed comprising mean abundance / site / day at 412 study sites for 127 dung beetle species. This matrix was fourth root transformed, converted to a correlation matrix for study sites, and subjected to hierarchical factor analysis using principal components to extract an optimum of five factors. Clusters of study sites with similar dung beetle assemblage structure and descriptive statistics were generated using the same procedure as in the biogeographical analysis. GLM one-way ANOVAs were used to determine the strength of separation in ordinal space both between clusters and along each factor.

Significant environmental differences between dung beetle regions and principal drivers of faunal differences were determined using General Linear and Regression Models (Statsoft, 2015 - Statistica v.12). GLM one-way ANOVAs and Tukey's HSD were used to detect differences between altitude, rainfall, temperature and relative sandiness at study sites in five dung beetle regions. Correlations between site values along each ordinal factor and log$_{10}$-transformed environmental data were determined using both GLM log-normal models and multiple regression from the General Regression module in Statistica v.12 (Statsoft, 2015).

NORTHERN CAPE SUB-REGIONS

Further hierarchical factor analyses were conducted on data matrices for each of five regional clusters of study sites in order to classify Northern Cape sub-regions. Data matrices comprised mean abundance / site / day at 138 study sites for 78 dung beetle species (Gariep Karoo), 102 sites x 94 species (Kalahari), 71 sites x 51 species (Bushmanland), 51 sites x 53 species (Upper Karoo) and 32 sites x 57 species (Gariep Stony Karoo). Treatment of the data and analysis of each matrix were the same as in the regional analysis except that factorization was limited to three (Gariep Karoo, Kalahari) or two. In the Gariep Karoo and Kalahari, GLM one-way ANOVAs and Tukey's HSD were used to detect differences between altitude, rainfall, temperature and relative sandiness at study sites in three sub-regions. For Bushmanland, Upper Karoo and Gariep Stony Karoo, t tests were used to detect differences between environmental parameters in sub-regions.

REGIONAL FAUNAL CHARACTERISTICS

EstimateS Version 9.1.0 (Colwell, 2013) was used to measure exponential Shannon-Wiener alpha diversity (expH') for each study site. Values for numbers of species and expH' per site were meaned for each of the five Northern Cape dung beetle regions defined by ordination. Significance of regional differences in mean values were determined using GLM one-way ANOVAs and Tukey's HSD.

As patterns shown by uncommon species were poorly supported or because biogeographical and functional data were unavailable, several faunal analyses were conducted on only the 60 numerically-dominant species that comprised >99% of total abundance at the 412 study sites. Abundance data for these species were used to determine proportional composition of biogeographical species groups in each North Cape dung beetle region. . As abundance differed between each region, proportional composition was standardized by using percentage abundance values.

Bias in the occurrences of the 60 numerically-dominant species between Northern Cape dung beetle regions was analyzed using multiple dimensional scaling (MDS) (Statsoft, 2015 - Statistica v.12). The data matrix comprised square root-transformed, mean abundance / trap / day shown by the 60 species across five regions. Two dimensions were specified for the analysis. On the ordination plot, a minimum spanning tree was fitted to assist interpretation of clustering. This was calculated by the MST module of the computer package, Arlequin v3.1 (Excoffier *et al.*, 2006) using a distance matrix generated by Statistica and the adjusted Kruskal algorithm from Arlequin.

Differences in functional composition of assemblages between Northern Cape dung beetle regions were also studied using data for the 60 numerically-dominant species. These taxa were classified according to three dry body weight classes ($<10^{-1}$, 10^{-1} to 10^{-2}, $>10^{-2}$ mg), three dung-exploitation habits (kleptocoprid, tunneler, ball roller), and two diel activity patterns (flight activity in darkness or daylight). Classification data were obtained from published results, measurements, observations, and estimates. This classification generated 10 proportional abundance values for the functional composition of each assemblage, which were used to measure functional diversity in each region (Shannon entropy). Similarity in functional composition between regions was determined by cluster analysis of a data matrix comprising 10 square root-transformed percentage values for each of five regions. The similarity matrix was calculated using the Bray-Curtis similarity coefficient and subjected to clustering by group average linking using Primer 5 Version 5.2.9 (Primer-E Ltd, 2002).

RESULTS

SPECIES POOL AND BIOGEOGRAPHY

The Northern Cape species pool comprised 127 species of scarabaeine dung beetles. Six biogeographical groups were defined for 113 of these species by Hierarchical Factor Analysis of their climatic distribution patterns across Southern Africa (Table 1, Fig. 2). The six groups accounted for 88.9% of total variance and were defined as Northeast Savanna, Kalahari, Highveld Grassland, Southwest Arid, Southwest Arid (south), and Winter / Bimodal Rainfall. Shared variance represented by secondary factor S1 showed that there was appreciable overlap between the two Southwest Arid species groups and the Kalahari group (Table 1). There was also

appreciable overlap (S2) between the Northeast Savanna and Kalahari groups, which overlapped with the Winter / Bimodal Rainfall group, respectively, along the south or west coasts. Unique variance represented by P factors was 20-37% in four arid and/or savanna groups but much higher in the Winter / Bimodal Rainfall group (P6: 69%) and extreme in the Highveld Grassland group (P3: 98%).
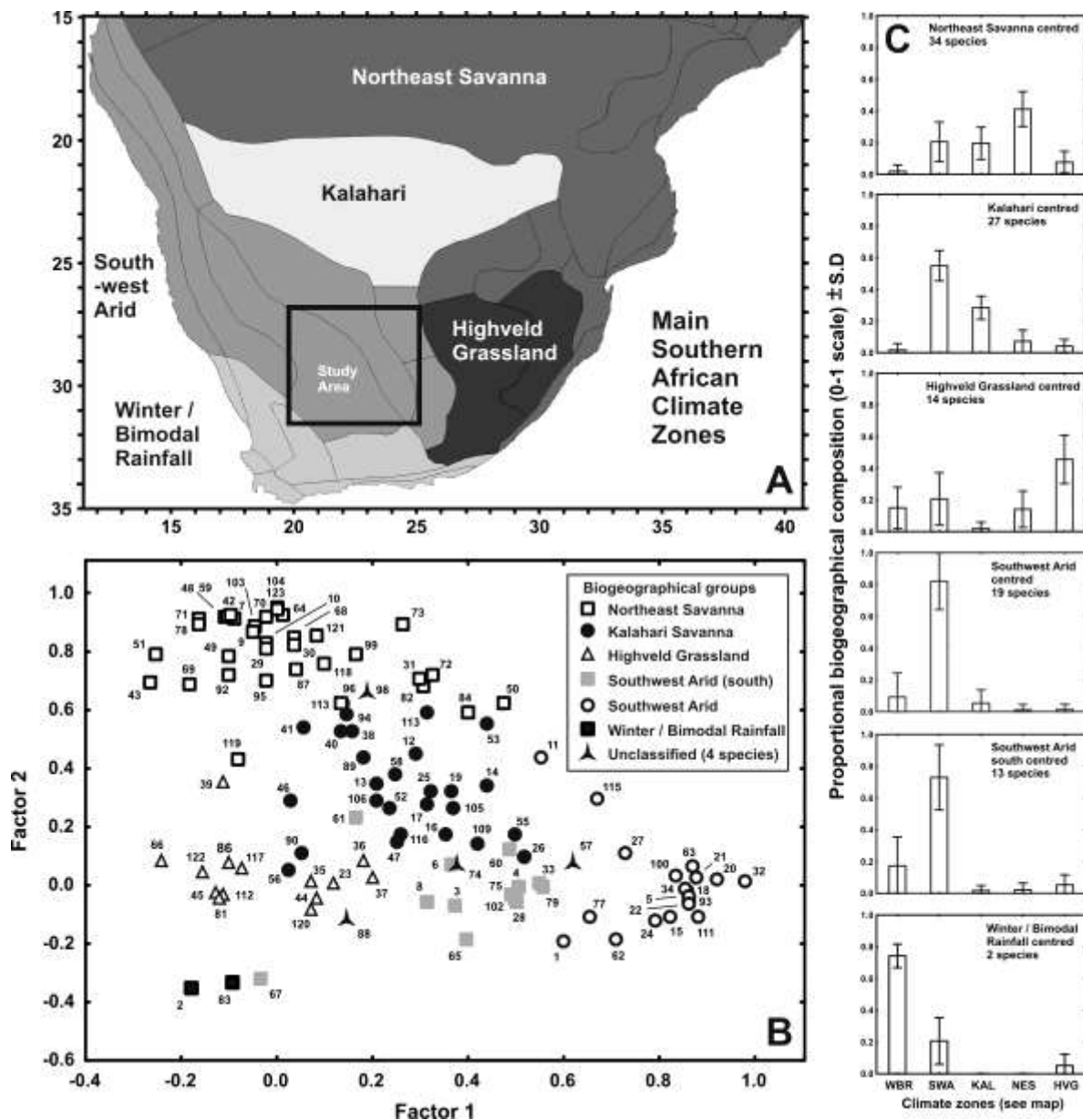
Figure 2. A. Main climatic regions of Southern Africa (modified from Walter & Lieth, 1964). B. Ordination plot showing distances between the Southern African climatic distributions of 113 taxa from the Northern Cape species pool of 127 species (see Table S3 for key). C. Bar diagrams showing mean proportional climatic bias in six biogeographical species groups (0-1 scale; WBR = Winter / Bimodal Rainfall, SWA = Southwest Arid, SWS = Southwest Arid (south), KAL = Kalahari, NES = Northeast Savanna, HVG = Highveld Grassland).

Table 1. Proportional distribution of variance within clusters (0-1) represented by correlations (r^2) between oblique factors (clusters) and orthogonal extended factors derived from hierarchical factor analysis of climatic distribution data for 113 dung beetle species (four unclassified).

Extended Factors*	Coefficient of determination (r^2)						Biogeographical Group
	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5	Cluster 6	
S1	0.63	0.05	0.02	0.57	0.79	0.00	Arid Southwest
S2	0.00	0.68	0.01	0.21	0.01	0.31	Moist NE, E and S
P1	0.37	0	0	0	0	0	Southwest Arid
P2	0	0.27	0	0	0	0	Northeast Savanna
P3	0	0	0.98	0	0	0	Highveld
P4	0	0	0	0.22	0	0	Kalahari
P5	0	0	0	0	0.20	0	SW Arid (South)
P6	0	0	0	0	0	0.69	Winter Rainfall
% variance^	49.9	24.1	12.6	6.8	4.3	2.7	Total 88.9%
N species	19	34	14	27	13	2	
Biog. group	SW Arid	NE Sav.	Highveld	Kalahari	SW Arid S.	Winter Rain.	

*S1, S2 = Secondary factors (shared variance), P1-P6 = Primary factors (unique variance), single "0" = no correlation at six places of decimals; sum of r^2 occasionally >1 due to rounding up.

^Proportional variance derived from eigenvalues.

NORTHERN CAPE REGIONS

Five regional faunas were defined across the transition zone by Hierarchical Factor Analysis of abundance data for 412 dung beetle assemblages (Figs 1B, 3; Tables 2, 3). The five regions included a minimum of 32 and a maximum of 138 assemblages each showing significantly high loadings along a single factor (Factors 1-5) with only 18 assemblages remaining unclassified. Within ordinal space, mean separation of factor loadings for regional clusters was highly significant although there was some overlap (Table 2). Four regions extended across the Nama Karoo, mainly to the south of the River Orange, whereas the fifth encompassed the southwest Kalahari, mostly to the north of the river (Fig. 1B). Shared variance represented by secondary factors (S1, S2) showed that faunal overlap represented by Factor S1 (Table 3) did not extend to the cooler Upper Karoo (0%) but was influential to varying degrees in other Karoo regions and in the Kalahari. To the converse, faunal

Table 2. Mean (±S.D.) ordinal loadings for clusters (Fig. 3) with results for GLM one-way ANOVAs showing significance of mean distances (***P <0.001) between dung beetle assemblage structure in five Northern Cape regions.

A. Rows	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5	F value $_{(df)}$
Factor 1	**0.651 ±0.089[a]**	0.101 ±0.121[d]	0.274 ±0.140[b]	0.281 ±0.147[b]	0.221 ±0.189[c]	294.33*** $_{(4, 685)}$
Factor 2	0.104 ±0.137[b]	**0.770 ±0.139[a]**	0.136 ±0.159[b]	-0.031 ±0.061[c]	0.144 ±0.185[b]	492.43*** $_{(4, 505)}$
Factor 3	0.257 ±0.092[b]	0.181 ±0.148[c]	**0.748 ±0.133[a]**	0.047 ±0.087[d]	0.233 ±0.158[bc]	317.40*** $_{(4, 345)}$
Factor 4	0.295 ±0.145[b]	-0.056 ±0.045[e]	0.053 ±0.070[d]	**0.760 ±0.104[a]**	0.125 ±0.139[c]	449.74*** $_{(4, 250)}$
Factor 5	0.230 ±0.137[c]	0.158 ±0.180[c]	0.347 ±0.114[b]	0.197 ±0.151[c]	**0.593 ±0.089[a]**	51.94*** $_{(4, 155)}$
B. Columns						
Factor 1	a	b	c	b	b	
Factor 2	c	a	d	e	c	
Factor 3	b	b	a	d	b	
Factor 4	b	c	e	a	c	
Factor 5	b	b	b	c	a	
$F_{(df 4, 389)}$	370.21***	529.02***	275.57***	455.30***	47.32***	
Region	Gariep Karoo	Kalahari	Bushmanland	Upper Karoo	Gariep Stony Karoo	

Values followed by a different letter in rows (A) or columns (B) differed significantly (P <0.05, Tukey's HSD).

overlap represented by Factor S2 did not extend to the deep sands of the Kalahari (0%) but was influential to varying degrees in all Karoo regions. Unique variance represented by primary factors (P1-P5) was similar between Karoo regions (21-30%) but much higher in the single Kalahari region (60%) (Table 3).

Table 3. Proportional distribution of variance within clusters (0-1) represented by correlations (r^2) between oblique factors (clusters) and orthogonal extended factors derived from hierarchical factor analysis of abundance data for 412 dung beetle species assemblages.

Extended Factors*	Coefficient of determination (r^2)					Northern Cape Region
	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5	
S1	0.25	0.40	0.65	0.00	0.50	Kalahari and Karoo
S2	0.54	0.00	0.11	0.71	0.28	Nama Karoo
P1	0.21	0	0	0	0	Gariep Karoo
P2	0	0.60	0	0	0	Kalahari
P3	0	0	0.25	0	0	Bushmanland Karoo
P4	0	0	0	0.30	0	Upper Karoo
P5	0	0	0	0	0.22	Gariep Stony Karoo
% variance^	45.2	17.2	7.9	3.7	3.3	Total 74.2%
N samples	138	102	71	51	32	
NC Region	Gariep	Kalahari	Bushman.	Upper	Gariep Stony	

*S = Secondary factors (shared variance), P = Primary factors (unique variance), single "0" = no correlation at six places of decimals; sum of r^2 occasionally >1 due to rounding up.

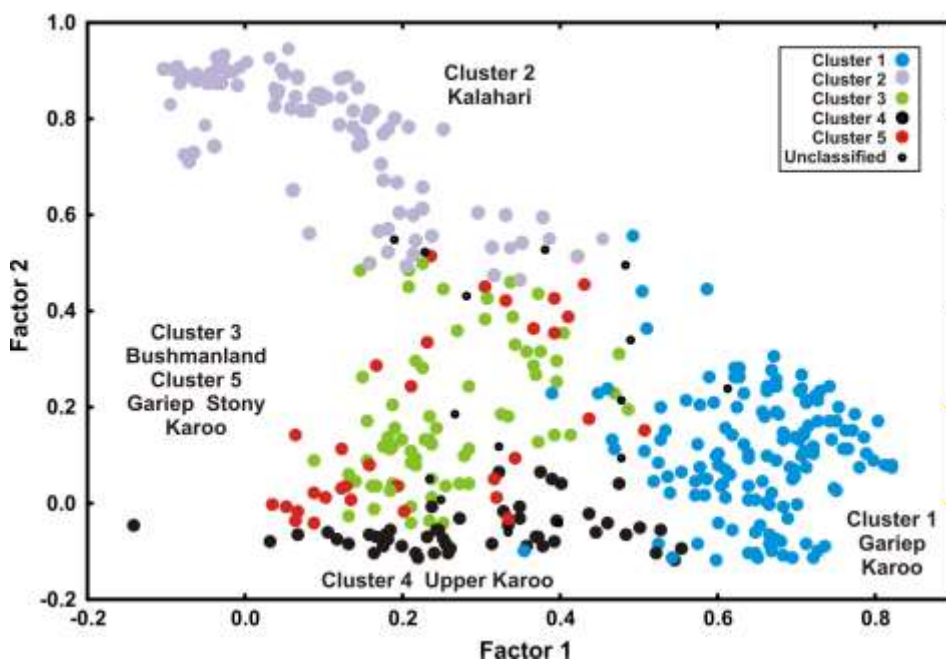^Proportional variance derived from eigenvalues.

Figure 3. Ordination plot showing the distance between dung beetle assemblage structure at 412 study sites in the Northern Cape with classification into five regional clusters.

REGIONS AND ENVIRONMENT

Environmental factors differed significantly between Northern Cape dung beetle regions (Table 4) reflecting differences in topography, gradients in rainfall and temperature, and differences in edaphic character. Mean altitude varied by over 400 m between regions and was reflected by a 4 °C variation in annual temperature (max.

+ min. / 2). There was also a 140 mm difference in annual rainfall between regions, which is substantial when maximum mean rainfall for any region was 280.7 mm per annum. Mean percentage of sand grains in soils within regions reflected a mosaic of outlier dunes and sandy saline pans in a matrix of finer-grained soils in Karoo regions compared to the dominance of deep sands in the Kalahari region.

Table 4. Mean environmental data ± S.D. for each cluster of Northern Cape study sites classified by ordination of dung beetle assemblage structure.

Cluster and F number	Altitude (m)^	Annual rain (mm)^	Annual temp. (max+min/2) (^{o}C)^	Soil composition (% sand grains)^	Northern Cape Region
Cluster 1	1110.0 ± 111.0[b]	190.8 ± 28.9[b]	17.6 ± 1.4[c]	47.8 ± 14.9[b]	Gariep Karoo
Cluster 2	1053.0 ± 84.5[c]	194.8 ± 30.3[b]	19.2 ± 0.5[a]	82.8 ± 16.4[a]	Kalahari
Cluster 3	924.8 ± 79.2[d]	140.9 ± 22.5[c]	19.3 ± 0.7[a]	50.1 ± 19.8[b]	Bushmanland Karoo
Cluster 4	1330.7 ± 98.4[a]	280.7 ± 26.6[a]	15.2 ± 0.9[d]	47.1 ± 5.3[b]	Upper Karoo
Cluster 5	1058.8 ± 96.6[c]	193.9 ± 22.0[b]	18.6 ± 0.4[b]	50.4 ± 15.1[b]	Gariep Stony Karoo
$F_{(df\ 4,\ 389)}$	137.69***	194.24***	182.80***	92.95***	

***$P<0.001$, (GLM one-way ANOVA). ^Within columns, numbers followed by a different letter differed significantly ($P<0.05$ - Tukey's HSD).

Table 5. Influence of environmental attributes on dung beetle assemblage structure in Northern Cape regions (1. Gariep Karoo, 2. Kalahari, 3. Bushmanland Karoo, 4. Upper Karoo, 5. Gariep Stony Karoo).

Generalized Linear model^ Environmental attribute	Wald statistic $_{(df\ 1)}$				
	1. Gariep	2. Kalahari	3. Bushman.	4. Upper	5. Stony
Annual rainfall	3.35	87.66***	**444.91***	68.02***	20.17***
Annual temperature	17.75***	109.93***	79.76***	**186.75***	48.58***
Proportion of sand	58.24***	**152.54***	64.16***	77.83***	28.88***
Stoniness (categorical: 0 or 1)	6.90**	2.29	13.76***	5.19*	8.84**

General regression^^ Environmental attribute	$F_{(df\ 1,\ 408)}$ (+ positive; - negative relationship)				
	1. Gariep	2. Kalahari	3. Bushman.	4. Upper	5. Stony
Annual rainfall	14.15***$_{(-)}$	69.87***$_{(+)}$	**399.70***$_{(-)}$	29.45***$_{(+)}$	20.28***$_{(+)}$
Annual temperature	32.47***$_{(-)}$	291.36***$_{(+)}$	0.56 $_{(+)}$	**422.71***$_{(-)}$	71.11***$_{(+)}$
Proportion of sand	59.71***$_{(-)}$	**315.04***$_{(+)}$	84.24***$_{(-)}$	134.71***$_{(-)}$	55.71***$_{(-)}$

^ log normal model; ^^multiple regression (log$_{10}$ transformed environmental data on ordinate values for dung beetle assemblage structure (see Table 2)).

Although nearly all correlations between ordinate values and environmental factors showed significant correlations, some were greater than others (Table 5). In the case of the transition zone in the Orange River Valley, regions on the southern valley edge (clusters designated, Gariep Karoo and Gariep Stony Karoo), no particular environmental correlation stood out as a major influence on the separation of its dung beetle fauna from that of other regions although the Gariep Karoo was cooler and less sandy than the Kalahari, wetter than Bushmanland and warmer than the Upper Karoo whereas the Gariep Stony Karoo was wetter, warmer and stonier than the Gariep Karoo. However, in the case of the three regions extending to the periphery of the study area (Fig. 1), stand-out statistics related to high correlations between ordinate values and cooler temperature (Upper Karoo), lower rainfall (Bushmanland), or higher proportion of sand grains in soils (Kalahari). The incidence of sand versus finer-grained soils and stony versus deep soils defined by categorical on-site observations supports the differences between study sites (Table 6).

Table 6. Proportion of sand grains and stony soils in Northern Cape dung beetle regions.

Cluster	% Sand (average per site)	% stony sites	Total N sites
Gariep Karoo	43.2	34.5	138
Kalahari	98.0	14.7	102
Bushmanland	69.0	43.7	71
Upper Karoo	7.8	64.7	51
Gariep Stony	50.0	68.7	32

SUB-REGIONS AND ENVIRONMENT

Each defined Northern Cape dung beetle region was subdivided in two or three using ordination (Table 7). Faunal overlap of 70-80% (S1) was demonstrated between sub-regions and 20-30% unique variance (P1, P2, P3). The bulk of the sites in the Gariep Karoo sub-regions were situated along the lower, warmer, southern edge of the Orange River Valley (Cluster A) with a few sites at cooler higher altitude further south (Cluster B - mainly Farms 41-43, also Farms 54, 55, 58 sampled in cold weather) or to the southwest at the edge of the Upper Karoo (Cluster C - mainly Farms 28, 29, 33, 34, 36, 37). The three Kalahari sub-regions comprised the typical deep sand fauna to the north of the River Orange (Cluster D) and two edge faunas along the north and south margins of the Orange River Valley where conditions were less sandy and often stony (Cluster E - especially Farms 10, 12-14) or drier and less sandy on isolated dunes or saline pans (Cluster F - especially Farms 15, 16, 70, 72). The two Bushmanland sub-regions comprised higher, moister sites to the northeast of the region (Cluster H) and lower appreciably drier sites to the southwest (Cluster G - Farms 77, 78, 80-87). The two Upper Karoo sub-regions comprised lower warmer sites to the west / northwest of the region (cluster I) and higher cooler sites to the east / southeast (Cluster J - mainly Farms 20-27). The two Gariep Stony Karoo sub-regions show no clear environmental bias, only slight eastern spatial bias (Cluster K - especially Farms 46-48, 59) or a mixture of east and west study sites (Cluster L). Thus, from the transition zone to the periphery of the study area, three Northern Cape regions show an intensification of the principal environmental factors by which they are defined in terms of strength of correlation, i.e. from stony sands or lower proportions of sand grains to deep 90% sands (Kalahari), from lower warmer to higher cooler conditions (Upper Karoo), and from moister to drier conditions (Bushmanland).

FLORAL AND DUNG BEETLE REGIONS

The Northern Cape dung beetle regions showed both congruence and divergence from floral regions (Fig. 1B). Kalahari or Karoo trends shown by secondary ordination factors (S1, S2) reflected the division at floral biome scale between the Savanna and Nama Karoo (Table 3, Fig. 1B). S2 was only represented in the Karoo not the Kalahari (0%). S1 was represented in both biomes but not in the coolest Karoo region (Upper Karoo, 0%). Primary ordination factors reflected divisions at bioregion scale but there were some divergences. The two Kalahari floral bioregions comprised only one dung beetle region. By contrast, both of the Nama Karoo floral Bioregions (Bushmanland, Upper Karoo) were represented by dung beetle regions. But, a further intervening dung beetle region (Gariep Karoo) straddled the Bushmanland / Upper Karoo boundary south of the River Orange (Fig. 1B). A second superimposed dung beetle region (Gariep Stony Karoo) may represent drier and stony conditions within the Gariep Karoo.

Table 7. Sub-regional attributes of dung beetle assemblages within Northern Cape regions: (a) correlations (coefficient of determination - r^2) between oblique factors (clusters) and orthogonal extended factors derived from hierarchical factor analyses representing proportional distribution of variance (0-1) within clusters; (b) environmental attributes within sub-regions.

Gariep Karoo 138 samples (7 unclassified)

| | (a) Coeff. of determ. (r^2) | | | | (b) Mean environmental factors ± S.D. | | | | |
	S1*	P1*	P2*	P3*	Altitude m	Rainfall mm	Temp. °C	% sand	% stony
Cluster A	0.70	0.30	0	0	1058.5 ± 59.0[b]	180.7 ± 20.5[b]	18.2 ± 0.8[a]	49.2 ± 15.8	26.1
Cluster B	0.72	0	0.28	0	1256.9 ± 86.1[a]	243.2 ± 24.4[a]	15.4 ± 0.9[c]	49.6 ± 13.2	22.2
Cluster C	0.79	0	0	0.21	1205.1 ± 133.8[a]	188.1 ± 15.0[b]	16.8 ± 1.6[b]	43.0 ± 12.9	71.4
$F_{(df\ 2,\ 128)}$					65.78***	71.47***	65.07***	1.55	

Kalahari 102 samples (2 unclassified)

| | (a) Coeff. of determ. (r^2) | | | | (b) Mean environmental factors ± S.D. | | | | |
	S1	P1	P2	P3	Altitude m	Rainfall mm	Temp. °C	% sand	% stony
Cluster D	0.74	0.26	0	0	1070.6 ± 86.0[a]	199.8 ± 30.9[a]	19.2 ± 0.5[a]	90.3 ± 2.8[a]	1.8
Cluster E	0.80	0	0.20	0	1042.1 ± 97.0[ab]	192.7 ± 30.0[ab]	19.3 ± 0.6[a]	70.9 ± 23.3[b]	52.0
Cluster F	0.72	0	0	0.28	1013.1 ± 31.5[b]	179.7 ± 20.9[b]	18.9 ± 0.2[b]	75.1 ± 17.6[b]	5.9
$F_{(df\ 2,\ 97)}$					3.49*	3.15*	4.20**	20.23***	

Bushmanland 71 samples (1 unclassified)

| | (a) Coeff. of determ. (r^2) | | | (b) Mean environmental factors ± S.D. | | | | |
	S1	P1	P2	Altitude m	Rainfall mm	Temp. °C	% sand	% stony
Cluster G	0.80	0.20	0	885.8 ± 71.4	126.7 ± 16.7	19.4 ± 0.7	45.0 ± 14.7	33.3
Cluster H	0.80	0	0.20	984.3 ± 49.2	162.0 ± 22.8	19.0 ± 0.7	56.2 ± 19.4	57.1
$t_{(df\ 68)}$				6.36*	9.97**	2.76	2.46**	

Upper Karoo 51 samples

| | (a) Coeff. of determ. (r^2) | | | (b) Mean environmental factors ± S.D. | | | | |
	S1	P1	P2	Altitude m	Rainfall mm	Temp. °C	% sand	% stony
Cluster I	0.75	0.25	0	1388.5 ± 46.4	289.0 ± 17.8	14.7 ± 0.4	48.3 ± 5.0	62.5
Cluster J	0.75	0	0.25	1233.4 ± 85.0	266.8 ± 33.2	16.0 ± 0.9	45.2 ± 5.5	68.4
$t_{(df\ 49)}$				8.44**	3.12**	7.19***	2.07	

Gariep Stony Karoo 32 samples

| | (a) Coeff. of determ. (r^2) | | | (b) Mean environmental factors ± S.D. | | | | |
	S1	P1	P2	Altitude m	Rainfall mm	Temp. °C	% sand	% stony
Cluster K	0.70	0.30	0	1059.1 ± 95.6	197.5 ± 19.6	18.6 ± 0.3	49.9 ± 13.5	80.0
Cluster L	0.70	0	0.30	1042.3 ± 101.6	187.7 ± 25.3	18.7 ± 0.6	51.3 ± 18.2	50.0
$t_{(df\ 30)}$				0.47	1.23	0.56	0.24	

*S = Secondary factors (shared variance), P = Primary factors (unique variance), single "0" = no correlation at six places of decimals.

REGIONAL FAUNAL CHARACTERISTICS

There were clear between-region differences in number of species and diversity in the Northern Cape (Fig 4). Mean number of species per study site was much greater on the Kalahari deep sands than in the Nama Karoo

whereas it was slightly greater in the Gariep and Upper Karoo than in arid Bushmanland or Gariep Stony Karoo. Mean diversity per study site was more equitable between Kalahari and some Nama Karoo regions although again lower in Bushmanland and Gariep Stony Karoo. Species patterns varied from abundance confined to a single defined region to more equitable distribution between regions, although most showed patterns of bias to particular regions (Table S3). Out of 127 species recorded across the study area, 75 showed extreme bias to a single region (>80% of their total abundance) with most biased to the Kalahari (47), many fewer to the Upper Karoo (16) and least to the other three regions (Gariep Karoo: 6, Gariep Stony Karoo: 4, Bushmanland: 2).
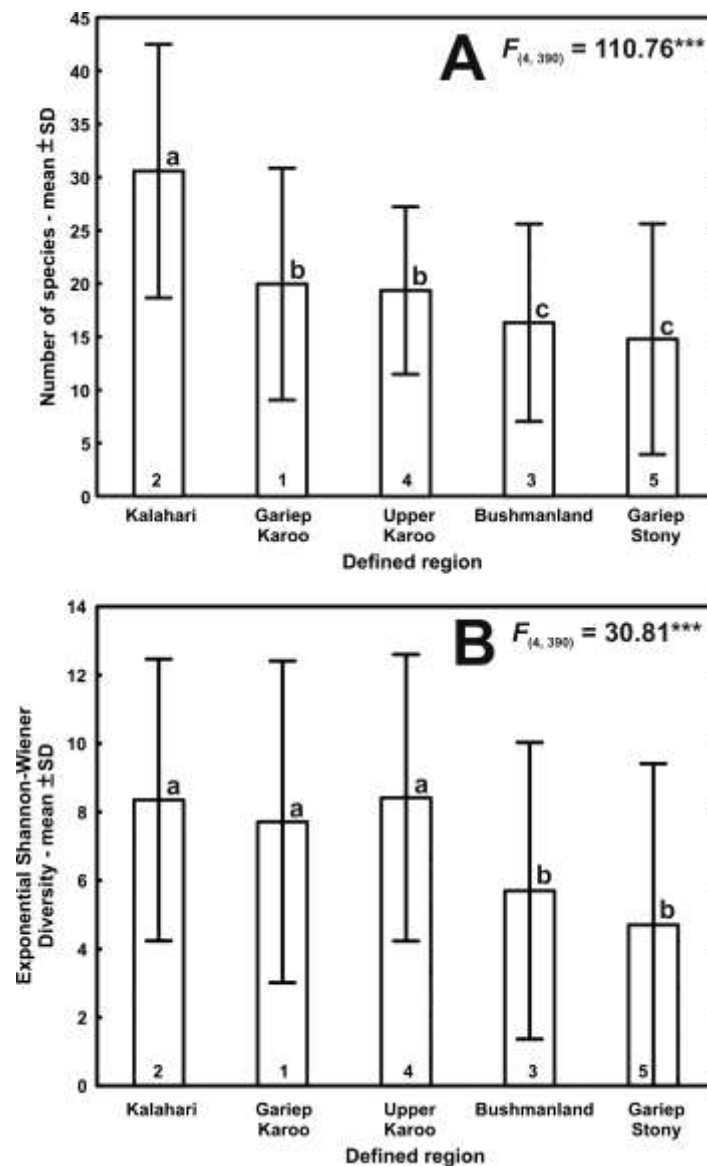

Figure 4. Mean number of dung beetle species (A) and mean exponential Shannon-Wiener diversity (expH') (B) per study site in each of five Northern Cape regions (results for GLM one-way ANOVAs are inset; columns identified by a different letter differ significantly (P <0.05, Tukey's HSD)).

The 60 most abundant species comprised from 98.3 to 99.7% of total abundance in each region and were considered to best define the principal species pool, regional, and local faunal characteristics. In terms of proportional abundance of the 60 most abundant species, there were strong differences in biogeographical composition between the five regions (Figs 2, 5). Northeast Savanna and Kalahari species groups dominated
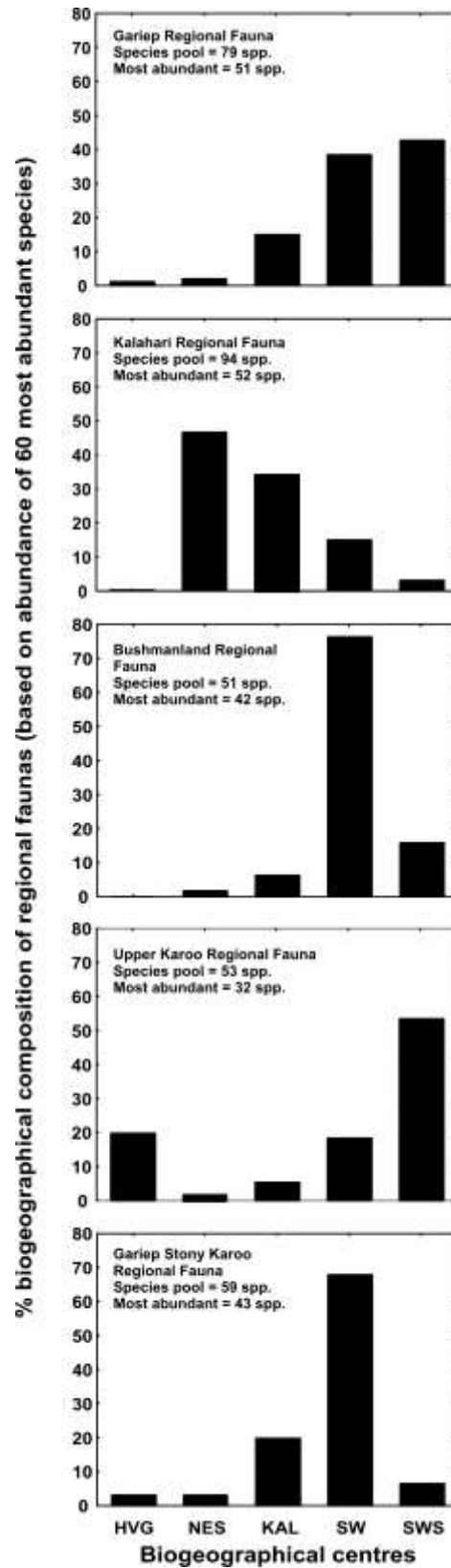
Figure 5. Proportional biogeographical composition within species assemblages of five regions across the Northern Cape transition zone derived from data for the 60 most abundant species (SWA = Southwest Arid, SWS = Southwest Arid (south), KAL = Kalahari, NES = Northeast Savanna, HVG = Highveld Grassland).
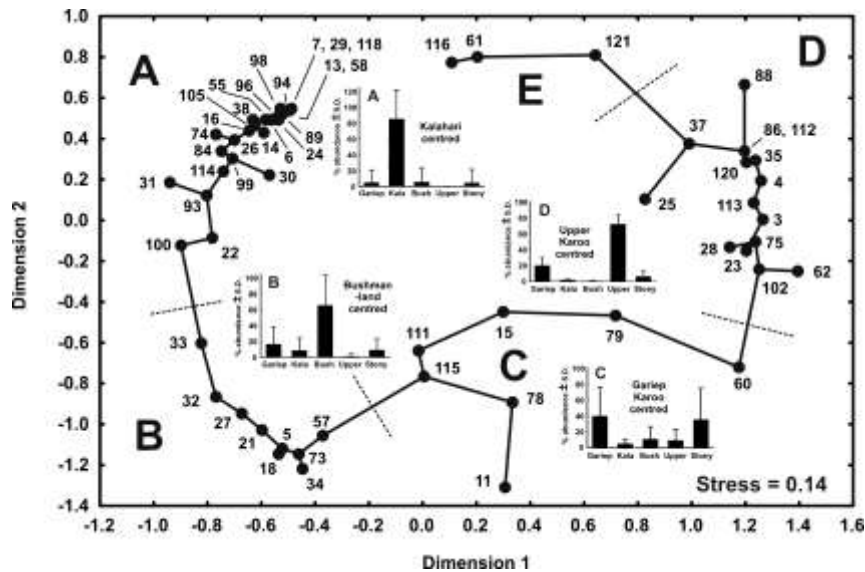
Figure 6. MDS ordination plot for the 60 most abundant species (99.1% total abundance) showing the distances between their abundance patterns across five Northern Cape regions. Patterns of similarity are supported by a minimum spanning tree along which three clusters and two scattered groups of species have been defined (key to species: Table S3). Bar diagrams for clusters and species groups show mean percentage abundance across Northern Cape regions.

only in the Kalahari region. The Southwest Arid species group dominated in arid Bushmanland and on the frequently stony soils of the Gariep Stony Karoo. The Southwest Arid species group and the Southwest Arid group with a cooler southern bias showed equal dominance in the Gariep Karoo whereas the Upper Karoo was dominated by Southwest Arid species with a cooler southern bias. However, all five regions showed appreciable representation by at least one other biogeographical group.

Three principal clusters of regional species patterns were defined for the 60 species (Fig. 6). These were centred on previously defined floral biomes and bioregions (Kalahari Savanna, Upper Karoo, Bushmanland Karoo) with greater distance between patterns of abundance for species centred in regions defined by the present dung beetle study (Gariep Karoo, Gariep Stony Karoo). Along the minimum spanning tree (Fig. 6), the 26 species of Pattern A showed from 46-100% of abundance on the deep sands of the Kalahari arid savanna. Of these, 17 showed over 90% of abundance in the Kalahari and the remainder variable degrees of occurrence in other regions but not the Upper Karoo. The nine species of Pattern B showed from 44-98% of abundance in arid Bushmanland. Of these only one showed more than 90% of abundance in the region and the remainder also variable degrees of occurrence in other regions but not the Upper Karoo. The 14 species of Pattern D showed from 40-100% of abundance in the cooler Upper Karoo. Of these five showed over 90% of abundance in the region and the remainder variable degrees of occurrence in other regions, mainly Gariep Karoo or Gariep Stony Karoo. The seven species defined as Pattern C were characteristic of Gariep Karoo or Gariep Stony Karoo (38-100% of abundance) but the greater distances between species mostly reflected a bias to either one or the other of the regions with five species showing >75% of overall abundance in the Gariep region. In general, negative to positive loadings represented a gradient from warmer to cooler conditions along Dimension 1 and from drier to moister conditions along Dimension 2.

For the 60 most abundant species, functional structure of assemblages varied between the five Northern Cape regions although functional diversity was only lower in Bushmanland (Fig. 7). Proportional similarity decreased from the Kalahari and Gariep Karoo into arid Bushmanland and cooler Upper Karoo. Small kleptocoprids ($<10^{-1}$ mg dry wt) were prominent in all regions as were medium-sized tunnelers ($10^{-1}$to 10^{-2} mg) and medium-sized ball rollers, the latter, particularly, well represented in arid Bushmanland. Small tunnelers were prominent only in the Kalahari and Gariep Stony Karoo as night flyers and Upper Karoo as day fliers. Large ball rollers ($>10^{-2}$ mg) were primarily most prominent in the cooler Gariep Karoo and Upper Karoo as day

flyers. Although 16 large tunneling species ($>10^{-2}$ mg) were represented across the study area, they were present in very low numbers and were not represented amongst the 60 most abundant species.
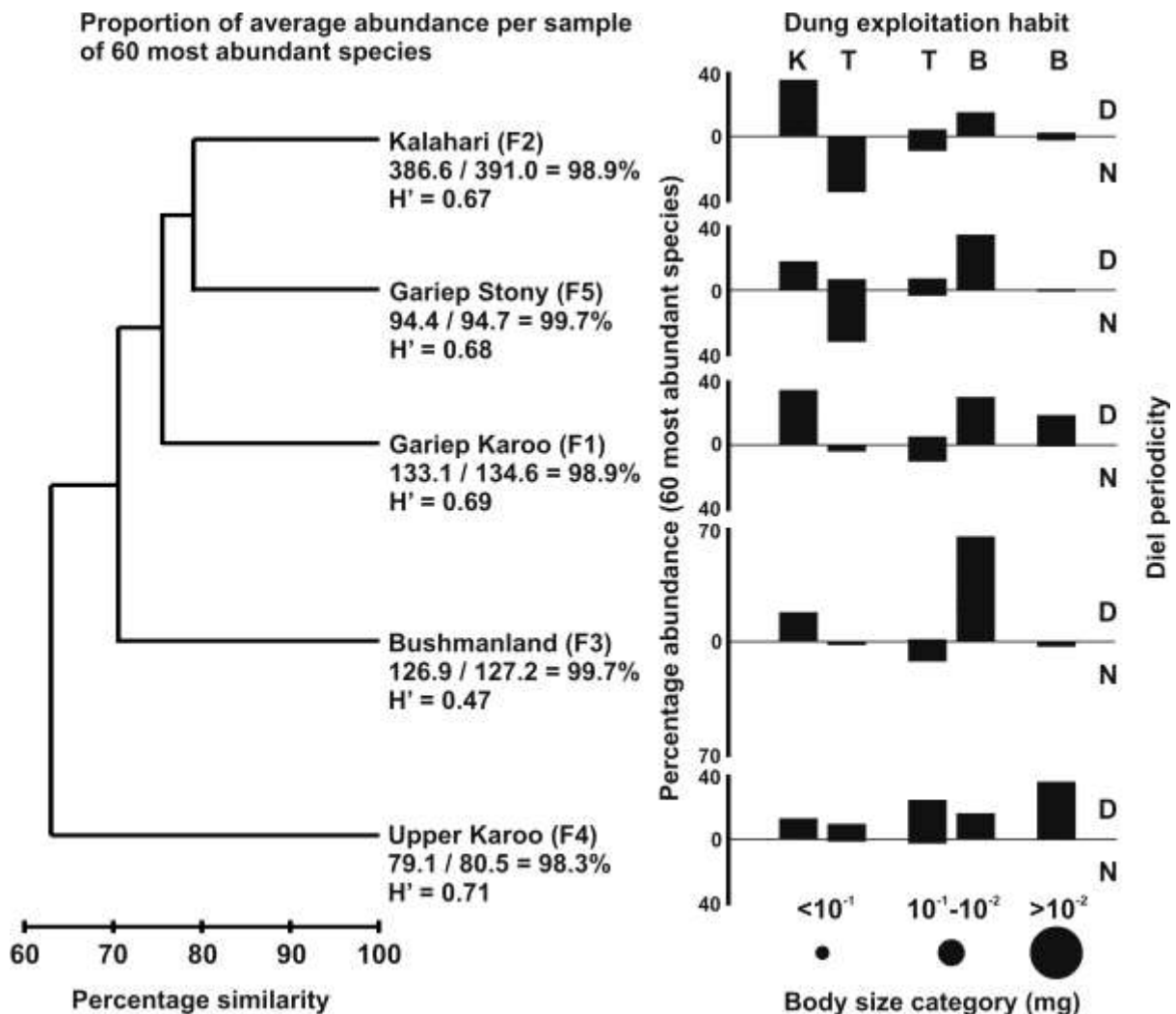

Figure 7. Patterns of functional structure in dung beetle assemblages of five Northern Cape regions. Bar diagrams are based on proportional abundance of the 60 most abundant species with axes comprising three body size classes ($<10^{-1}$ to $>10^{-2}$ mg, spots represent: 10^{-1}, 10^{-2}, 10^{-3} mg dry weight), three dung exploitation habits (K= kleptocoprid, T = tunneler, B = ball-roller) and two categories of diel flight activity (D = day, N = night). Dendrogram shows proportional similarity between patterns. Functional diversity indicated by Shannon entropy values (H').

DISCUSSION

HISTORY AND ENDEMISM

History on a geological age scale, overlies changing patterns of species numbers and diversity across spatial gradients that are subject to both regional and local processes (Ricklefs, 1987; Lobo *et al*., 2006; Mykrä *et al*., 2007). Historical influences on the Northern Cape are documented by recent literature, which shows how Miocene deposition of sand has modified edaphic character to the north in the Kalahari (Haddon & McCarthy, 2005). Climatic character across the entire area has also been modified by increased late Cenozoic polar glaciation (McKay *et al*., 2012) that is linked to increased upwelling of the cold Benguela current (Marlow *et al*., 2000; Petrick *et al*., 2015) and has driven Miocene to Plio-Pleistocene change in rainfall seasonality (Deacon, 1983) with increasing aridity (Tankard & Rogers, 1978) in much of southwestern Africa. Evidence is

offered by sedimentary mineral structure (Eze & Meadows, 2014), fossil pollen (Hoetzel *et al.*, 2015) and fossil foraminifera (Diekmann *et al.*, 2003). In particular, high latitude cooling caused Plio-Pleistocene northwards shift of climatic cells leading to the displacement of subtropical climate and the development of a winter rainfall system in the southwest (Deacon, 1983) that is perhaps partly reflected by low representation of subtropical / tropical C_4 grasses in the southwest (Dupont *et al.*, 2013) and north / south differences in sedimentary carbon accumulation along the southwest marine upwelling zone (Giraudeau *et al.*, 2002). The current observable southwest / northeast climatic trend from Mediterranean winter rainfall, aridity and mesic summer rainfall may be of long duration since relative stability in rainfall for the past 2.5 MY is indicated by carbon isotope records extracted from marine sediments off the mouth of the River Orange (Maslin *et al.*, 2012).

Whatever the precise chronology, historical events that have generated the present functional ecological setting are of sufficient age to have driven three centres of dung beetle endemism in the late summer rainfall climatic region. Whereas endemism reflects climatic drivers in the two southwest arid centres, both climatic and edaphic drivers would be responsible for endemism biased to the arid southwest edge of the Kalahari Basin. The division of southwest arid endemics into pan-southwest-centred and south-centred species groups reflects warmer, dryer versus cooler, moister climate in uplifted areas. Cooler areas of the Upper Nama Karoo near the Grassland biome also include highveld elements. Elements of the northeast, summer rainfall, savanna fauna are well-represented in the Kalahari but hardly any penetrate into the Nama Karoo. However, Kalahari-centred savanna elements are rather better represented in the north Nama Karoo where they occur on scattered outlier dunes and sandy pans but decrease in number into cooler and dryer regions. There is little influence from the southwestern, winter rainfall region in the late summer rainfall study area although some of the southwest Kalahari fauna is represented in the winter rainfall region along the sandy west coast (e.g. *Metacatharsius latifrons*, *Onitis confusus*).

There is no molecular phylogenetic analysis to support the claimed Miocene to Pleistocene age of endemism in southwest species centres although a primarily Miocene to Plio-Pleistocene age of diversification is claimed between and within many of the genera represented in the Northern Cape study area (Mlambo *et al.*, 2015). However, much of the endemism is centred on large arid or arid, sandy areas that extend well beyond Northern Cape. Only a single species (*Hyalonthophagus* sp.) may show a range confined to the study area on the uplands to the south of the River Orange, primarily in the Gariep Karoo. These results may reflect the geologically young age of the patterns.

SPECIES POOLS AND BIOGEOGRAPHY

Species pools defined from an arbitrary geographical area have been criticized for lack of objectivity (Carstensen *et al.*, 2014). However, the top-down methods (analysis of biogeographical patterns in large-scale spatial data) that they recommend for objectively defining the "biogeographical species pool" are useful only for identifying biogeographical regions. Although the centres of such regions would be expected to be dominated by the defined species pool, in the present study across a transition zone, regional groups of local species assemblages are shown to be composed of taxa from multiple biogeographical centres. Thus, as many species are not confined to particular areas but overlap beyond defined centres or boundaries into other regions, the present method that combines bottom up (small spatial scale definition of species pool) and top down approaches (analysis of biogeographical patterns shown by that pool of species using large-scale spatial data) is considered to be a better, more realistic and flexible approach to studies that are examining large-scale influences at small spatial scales.

The expanded and improved database for dung beetles in southern Africa generated climatic distribution data from which a single ordination defined six biogeographical centres for 113 species out of 127 recorded in the study area. A previous analysis of 104 species using an older, less-comprehensive database required three ordinations to define these centres (Davis *et al.*, 2008). However, it should be noted that no widespread species centre was defined in the present analysis and the Kalahari centre was not divided into widespread and southwest centred groups. Of the six centres defined by the present single ordination, five were

represented within the 60 most abundant species. The Winter / Bimodal Rainfall centre was represented by only two species occurring in low abundance in the Northern Cape.

Biogeographical composition of regional faunas strongly reflected the northeast / southwest trend in climate and edaphic character that developed in the Pliocene. Although the study area was entirely situated within the southwest arid, late summer rainfall region, only the Nama Karoo regions were dominated by southwest arid centred species. These regions differed in relative dominance between groups with widespread or southern bias in distribution according to warmer (Bushmanland, Gariep Stony Karoo), intermediate (Gariep Karoo) or cooler climate (Upper Karoo). The deep sands of the Kalahari savanna differed radically through dominance by northeast savanna and Kalahari centred groups with a small widespread southwest arid component. The Kalahari group component decreased into the Nama Karoo where soils were less frequently sandy with similar rain but cooler conditions (Gariep regions), even cooler and wetter conditions (Upper Karoo), or with similar temperatures but much more arid conditions (Bushmanland).

Size of the species pools strongly reflected the northeast / southwest trend in climate and edaphic character. Numbers of species declined significantly from the deep sands of the southwest Kalahari to the cooler, less sandy conditions of the Gariep Karoo and moister Upper Karoo and, declined further in the harsher conditions represented by warm but arid Bushmanland and lower frequency of deep soils in Gariep Stony Karoo. By contrast, alpha diversity was significantly lower only in the two ecologically harshest regions. It is known that deep sands support more dung beetle species than finer-grained soils (Davis, 1996) but this observation has to be weighed against effects of different climatic combinations in the Nama Karoo. Such declines across ecological gradients from apparently more favourable to potentially harsher ecological conditions are frequently observed in insect assemblages (Pérez-Sánchez *et al*., 2013; Tshikae *et al*., 2013c) although there are exceptions possibly related to asymmetric variability and interaction between factors such as aridity, soil type and / or temperature (Pfeiffer *et al*., 2003; Delsinne *et al*., 2010)**.**

ECOLOGICAL RESPONSES

Across the historically-generated environmental gradients, dung beetle assemblage structure shows clear patterns of unique or shared variance across different Northern Cape regions and strong correlations with climatic and edaphic factors. However, ordinal loadings may also reflect both landscape heterogeneity and productivity indicated by different vegetation structure across the transition zone (grass, shrubs and trees in different proportions and different cover densities). On deep sands in neighbouring Botswana, dung beetle assemblages were correlated to a mix of abiotic factors, vegetation structure and productivity in terms of dung-producing mammal diversity although temperature and rainfall tended to be the strongest correlates (Tshikae *et al*., 2013a). By contrast, functional structure in pan-Mediterranean ants was more strongly correlated to productivity and vegetation structure than abiotic correlates (Arnan *et al*., 2014). It seems likely that relative strength of correlations between abiotic factors and the biotic factors that they drive may vary between the study taxon, the spatial, trophic and temporal scale of the study, and the focus on measures related to either species identity (species numbers, diversity) or functional attributes that may or may not be subject to phylogenetic relatedness.

In the present study, the regional and sub-regional analyses show how several principal abiotic factors drive assemblage structure along major edaphic and climatic axes of Miocene to Pliocene origin. Sandy soils, cooler temperatures, and extremely low rainfall, were major drivers characterizing the Kalahari, Upper Karoo and Bushmanland regions, respectively. In the centre of the study area, towards the Orange River Valley, results for the Gariep Karoo Region reflect no particular dominant abiotic factors. However, within each region, patterns of positive or negative correlations with rainfall, temperature and proportion of sand gains in soils, differed from all other Northern Cape regions.

Failure to support or reject contrasting hypotheses has driven a progression from the use of species numbers and diversity to define assemblage composition towards the use of functional traits combined with analyses of phylogenetic relatedness that may better distinguish between historical, deterministic and stochastic

drivers of assemblages (Pavoine & Bonsall, 2011). Although it would be useful to analyze the current data set employing a phylogenetic and functional approach, sufficiently detailed functional and phylogenetic data are currently unavailable. However, a basic functional analysis has been conducted that shows clear differences between regions. It also indicates decreased functional diversity with increasing aridity across the Pliocene rainfall gradient due to the dominance of small ball rollers in Bushmanland.

FAUNAL RESPONSES

Historically generated trends in climatic and edaphic factors result in differences between the species characterizing each Northern Cape region. Although standardized data for soil associations of Northern Cape dung beetle fauna are unavailable, many studies have demonstrated how dung beetle species may show association with particular soil types (Davis, 1996). This has undoubtedly influenced centring and endemism of many species on the deep sands of the Kalahari, particularly as assemblages of all Karoo regions were negatively correlated with sandy soils. This suggests that many of the characteristic Nama Karoo species are biased to the finer-grained soils that dominate in the region (FAO, 2012). However, there were a few endemic *Scarabaeus* (*Scarabaeolus*) species centred in the Nama Karoo. These species were mainly associated with the outlier dunes or loamy sands of saline pans that are scattered across the region (*S. pabulator*, *S. karrooensis* in Bushmanland; *S. fritschi* in the Gariep Karoo). However, most characteristic Nama Karoo species are probably separated essentially by climatic factors as implied by the biogeographical associations of species (cool, warm dry, or arid-adapted).

Functional structure of assemblages shows from 21-37% dissimilarity across the five Northern Cape regions even though the entire transitional study area lies within the arid late summer rainfall region where the natural mammal fauna would have been biased to pellet-dropping taxa as in the neighbouring arid southwest of Botswana (Tshikae *et al.*, 2013b). Thus, large tunnelling species are not represented in the 60 most abundant species since they are more characteristic of large dung types dropped by megaherbivores in moister areas (Tshikae *et al.*, 2013a). However, 16 species are present in low abundance. Abundant tunnelers are represented primarily by medium-sized *Cheironitis*, *Phalops* (day-flying) and *Metacatharsius* (night-flying) or by small-bodied *Onthophagus* (night-flying) in the Kalahari and Gariep Stony Karoo. The representation of small-bodied, onthophagine kleptocoprids in all regions may reflect the diverse ball-rolling fauna. Large diurnal ball rollers of the tribe, Scarabaeini, are a dominant component only in the cooler, moister, Upper Karoo and Gariep Karoo, possibly related to thermoregulation. However, medium-sized diurnal ball rollers are well-represented in all regions but are dominant in hotter regions, particularly, Bushmanland, which is the centre of distribution for three heat-tolerant *Gymnopleurus* species (*G. asperrimus*, *G. humanus*, *G. andreaei*). Medium-sized ball-rolling *Scarabaeus* (*Scarabaeolus*) species were better represented on cooler, moister sands of the Kalahari, especially immediately after rain. Their lower representation in Bushmanland may be due both to the more arid climate and the restricted occurrence of sand. Overall the cooler Upper Karoo fauna is primarily diurnal whereas the remaining regions show a primarily diurnal kleptocoprid and ball-rolling fauna with tunnelers mainly night-flying. It is likely that Miocene to Pleistocene changes in climate and edaphic character have influenced differences in functional structure favouring taxa with suitable physiological and behavioural attributes. However, productivity is, undoubtedly, also important as in Botswana (Tshikae *et al.*, 2013c) where dung type diversity is low in the arid southwest and increases to the moister northeast according to diversity of dropping mass (large cohesive mass, collection of large boluses or small pellets) and physico-chemical composition related to diet and digestive system (different spectra of released volatiles, fine to coarse-fibred) (Tshikae *et al.*, 2013b).

FLORAL AND DUNG BEETLE REGIONS

The present study provides a better geographical coverage of the patterns and therefore improves on the findings of Davis *et al*. (2008). At the edge of the Kalahari, significance of dung beetle variation on isolated dunes to the south of the River Orange is reduced from regional (Davis *at al*., 2008) to sub-regional scale. At the southern

edge of the Orange River Valley, upland sites in northern Bushmanland were previously cited as the "Upper Karoo" dung beetle region (Davis *at al*., 2008) but now comprise the western end of a region defined as "Gariep Karoo". This straddles the boundary between the Bushmanland and Upper Karoo floral bioregions (Mucina & Rutherford, 2006). The Gariep Karoo fauna differs from that on uplands further to the east that now become the new Upper Karoo dung beetle region. Thus, differences remain between floral bioregions and Northern Cape dung beetle regions although large parts of the floral transition between Savanna and Nama Karoo represent areas of error in the predictive classification and regression tree developed by Mucina and Rutherford (2006).

CONCLUSION

The current setting of the Northern Cape study area has been driven primarily by Miocene to Plio-Pleistocene geological and climatic events. Although it straddles the transition zone between the Savanna and Nama Karoo Biomes and approaches close to the Highveld Grassland Biome in the southeast, it falls entirely within the arid late summer rainfall region. Even so, the Northern Cape species pool shows multiple biogeographical origins along a southwest / northeast climatic gradient and is selected across the transition zone according to climatic differences (rainfall and temperature modified by topography), ecological conditions (edaphic, microhabitat), and biotic interactions according to functional attributes (competitive ability conferred by dung exploitation habit, body size differences, and physiological condition).

ACKNOWLEDGEMENTS

REFERENCES

Arnan X, Cerda X, Retana J. 2014. Ant functional responses along environmental gradients. *Journal of Animal Ecology* **87:** 1398–1408.

Bornemissza GF. 1969. A new type of brood care observed in the dung beetle *Oniticellus cinctus* (Scarabaeidae). *Pedobiologia* **9:** 223–225.

Carnicer J, Díaz-Delgado J. 2008. Geographic differences between functional groups in patterns of bird species richness in North America. *Acta Oecologica* **33:** 253–264.

Carnicer J, Brotons L, Stefanescu C, Peñuelas J. 2012. Biogeography of species richness gradients: linking adaptive traits, demography and diversification. *Biological Reviews* **87:** 457–479.

Carstensen DW, Lessard J-P, Holt BG, Borregaard MK, Ragbek C. 2013. Introducing the biogeographic species pool. *Ecography* **36:** 1310–1318.

Colwell RK. 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. Available at http://viceroy.eeb.uconn.edu/estimates/

Dauteuil O, Bessin P, Guillocheau F. 2015. Topographic growth around the Orange River valley, southern Africa: A Cenozoic record of crustal deformation and climatic change. *Geomorphology* **233:** 5–19.

Davis ALV. 1996. Habitat associations in a South African, summer rainfall, dung beetle community (Coleoptera: Scarabaeidae, Aphodiidae, Staphylinidae, Histeridae, Hydrophilidae). *Pedobiologia* **40:** 260–280.

Davis ALV. 1997. Climatic and biogeographical associations of southern African dung beetles (Coleoptera: Scarabaeidae *s. str.*). *African Journal of Ecology* **35:** 10–38.

Davis ALV, Scholtz CH, Chown SL. 1999. Species turnover, community boundaries and biogeographical composition of dung beetle assemblages across an altitudinal gradient in South Africa. *Journal of Biogeography* **26:** 1039–1055.

Davis ALV, Scholtz CH, Deschodt C. 2008. Multi-scale determinants of dung beetle assemblage structure across abiotic gradients of the Kalahari–Nama Karoo ecotone, South Africa. *Journal of Biogeography* **35:** 1465–1480.

Davis ALV, van Aarde RJ, Scholtz CH, Guldemond RAR, Fourie J, Deschodt CM. 2013. Is microclimate-driven turnover of dung beetle assemblage structure in regenerating coastal vegetation a precursor to re-establishment of a forest fauna? *Journal of Insect Conservation* **17:** 565–576.

Deacon HJ. 1983. An introduction to the fynbos region, time scales and palaeoenvironments. Fynbos palaeoecology: a preliminary synthesis: 1–20.

Delsinne, T, Roisin Y, Herbauts J, Leponce M. 2010. Ant diversity along a wide rainfall gradient in the Paraguayan dry Chaco. *Journal of Arid Environments* **74:** 1149–1155.

De Wit MCJ, Bamford MK. 1993. Fossil wood from the Brandvlei area, Bushmanland, as an indication of palaeoenvironmental changes during the Cainozoic. *Palaeontology of Africa* **30:** 81–89.

Diekmann B, Fälker M, Kuhn G. 2003. Environmental history of the south-eastern South Atlantic since the Middle Miocene: evidence from the sedimentological records of ODP Sites 1088 and 1092. *Sedimentology* **50:** 511–529.

Doube BM. 1990. A functional classification for analysis of the structure of dung beetle assemblages. *Ecological Entomology* **15:** 371–384.

Dupont LM, Rommerskirchen F, Mollenhauer G, Schefuß E. 2013. Miocene to Pliocene changes in South African hydrology and vegetation in relation to the expansion of C_4 plants. *Earth and Planetary Science Letters* **375:** 408–417.

Excoffier L, Laval G, Schneider S. 2006. Arlequin ver. 3.1. An integrated software package for population genetics data analysis. Available at: http://cmpg.unibe.ch/software/arlequin3

Eze PN, Meadows ME. 2014. Mineralogy and micromorphology of a late Neogene paleosol sequence at Langebaanweg, South Africa: Inference of paleoclimates. *Palaeogeography, Palaeoclimatology, Palaeoecology* **409:** 205–216.

FAO. 2012. FAO/IIASA/ISRIC/ISSCAS/JRC Harmonized world soil database (version 1.21).

Fayle TM, Eggleton P, Manica A, Yusah KM, Foster WA. 2015. Experimentally testing and assessing the predictive power of species assembly rules for tropical canopy ants. *Ecology Letters* **18:** 254–262.

Giraudeau J, Meyers PA, Christensen BA. 2002. Accumulation of organic and inorganic carbon in Pliocene–Pleistocene sediments along the SW African margin. *Marine Geology* **180:** 49–69.

Gotelli NJ, Ellison AM. 2002. Assembly rules for New England ant assemblages. *Oikos* **99:** 591–599.

Haddon IG, McCarthy TS. 2005. The Mesozoic–Cenozoic interior sag basins of Central Africa: The Late-Cretaceous–Cenozoic Kalahari and Okavango basins. *Journal of African Earth Sciences* **43:** 316-333.

Hanski I, Cambefort Y. 1991. Competition in dung beetles. In: Hanski I, Cambefort Y, eds. *Dung beetle ecology*. Princeton: Princeton University Press, 305–329.

Hawkins BA, Field R, Cornell HV, Currie DJ, Guégan J-F, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Porter EE, Turner JRG. 2003. Energy, water, and broad-scale geographic patterns of species richness. *Ecology* **84:** 3105–3117.

Hodkinson ID. 2005. Terrestrial insects along elevation gradients: species and community responses to altitude *Biological Reviews* **80:** 489–513.

Hoetzel S, Dupont LM, Wefer G. 2015. Miocene–Pliocene vegetation change in south-western Africa (ODP Site 1081, offshore Namibia). *Palaeogeography, Palaeoclimatology, Palaeoecology* **423:** 102–108.

Lobo JM, Davis ALV. 1999. An intercontinental comparison of dung beetle diversity between two mediterranean-climatic regions: local versus regional and historical influences. *Diversity and Distributions* **5:** 91–103.

Lobo JM, Hortal J, Cabrero-Sañudo FJ. 2006. Regional and local influence of grazing activity on the diversity of a semi-arid dung beetle community. *Diversity and Distributions* **12:** 111–123.

McKay R, Naishar T, Carter L, Riesselman C, Dunbar R, Sjunneskogd C, Winter D, Sangiorgif S, Warren C, Pagani M, Schoutenh S, Willmotth V, Levy R, DeConto R, Powel RD. 2012. Antarctic and southern ocean influences on late Pliocene global cooling. *Proceedings of the National Academy of Sciences* **109:** 6423–6428.

Marlow JR, Lange CB, Wefer G, Rosell-Melé A. 2000. Upwelling intensification as part of the Pliocene-Pleistocene climate transition. *Science* **280:** 2288–2291.

Maslin MA, Pancost RD, Wilson KE, Lewis J, Trauth MH. 2012. Three and half million year history of moisture availability of South West Africa: Evidence from ODP site 1085 biomarker records. *Palaeogeography, Palaeoclimatology, Palaeoecology* **317-318:** 41–47.

Maud RR. 2012. Macroscale geomorphic evolution. In: Holmes P, Meadows M, eds. *Southern African Geomorphology: Recent Trends and New Directions*. Bloemfontein: Sun Media, 5–21.

Mlambo S, Sole CL, Scholtz CH. 2015. A molecular phylogeny of the African Scarabaeinae (Coleoptera: Scarabaeidae). *Arthropod Systematics & Phylogeny* **73:** 303–321.

Mucina L, Rutherford MC. 2006. The vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* **19:** 1–807.

Mykrä HJ, Muotka T. 2007. Scale-related patterns in the spatial and environmental components of stream macroinvertebrate assemblage variation. *Global Ecology and Biogeography* **16:** 149–159.

Partridge TC, Maud, RR. 1987. Geomorphic evolution of Southern Africa since the Mesozoic. *South African Journal of Geology* **90:** 179–208.

Pavoine S, Bonsall MB. 2011. Measuring biodiversity to explain community assembly: a unified approach. *Biological Reviews* **86:** 792–812.

Pérez-Sánchez AJ, Lattke JE, Viloria AL. 2013. Patterns of ant (Hymenoptera: Formicidae) richness and relative abundance along an aridity gradient in western Venezuela. *Neotropical Entomology* **42:** 128–136.

Petrick B, McClymont EL, Felder S, Rueda G, Leng ML, Rosell-Melé A. 2015. Late Pliocene upwelling in the Southern Benguela region. *Palaeogeography, Palaeoclimatology, Palaeoecology* **429:** 62–71.

Pfeiffer M, Chimedregzen L, Ulykpan K. 2003. Community organization and species richness of ants (Hymenoptera/Formicidae) in Mongolia along an ecological gradient from steppe to Gobi desert. *Journal of Biogeography* **30:** 1921–1935.

Primer-E Ltd 5. 2002. Primer 5 for windows version 5.2.9.

Ricklefs RE. 1987. Community diversity: Relative roles of local and regional processes. *Science* **235:** 167–171.

Statsoft Inc. 2015. STATISTICA (data Analysis Software System), Version 12.

Stein A, Kreft H. 2015. Terminology and quantification of environmental heterogeneity in species-richness research. *Biological Reviews* **90:** 815–836.

Stokes S, Haynes G, Thomas DSG, Horrocks JL, Higginson M, Malifa M. 1998. Punctuated aridity in southern Africa during the late glacial cycle: The chronology of linear dune construction in the northeastern Kalahari. *Palaeogeography, Palaeoclimatology, Palaeoecology* **137:** 305–322.

Tankard AJ, Rogers J. 1978. Late Cenozoic palaeoenvironments on the west coast of Southern Africa. *Journal of Biogeography* **5:** 319–337.

Tshikae BP, Davis ALV, Scholtz CH. 2013a. Dung beetle assemblage structure across the aridity and trophic resource gradient of the Botswana Kalahari: patterns and drivers at regional and local scales. *Journal of Insect Conservation* **17:** 623–636.

Tshikae BP, Davis ALV, Scholtz CH. 2013b. Does an aridity and trophic resource gradient drive patterns of dung beetle food selection across the Botswana Kalahari? *Ecological Entomology* **38:** 83–95.

Tshikae BP, Davis ALV, Scholtz CH. 2013c. Species richness – Energy relationships and dung beetle diversity across an aridity and trophic resource gradient. *Acta Oecologica* **49:** 71–82.

Tuomisto H, Zuquim G, Cárdenas G. 2014. Species richness and diversity along edaphic and climatic gradients in Amazonia. *Ecography* **37:** 1034–1046.

Tyson, PD. 1986. Climatic change and variability in Southern Africa. Cape Town: Oxford University Press.

Walter H, Lieth H. 1964. Klimadiagramm-Weltatlas. Jena: Gustav Fischer.

Supporting Information

Table S1. A. Distribution of study sites between biomes, bioregions and vegetation units of the Northern Cape with notes on soil and vegetation structure. B. Origin of biogeographical data for Southern Africa.

A.

A total of 96 study sites were in the Kalahari portion of the Savanna Biome as defined by Mucina & Rutherford (2006). These comprised 45 sites in the Eastern Kalahari Bushveld Bioregion (SVk) primarily on two vegetation units, Olifantshoek Plains Thornveld (SVk13) (33 sites) and Gordonia Plains Shrubland (SVk16) (10 sites), but also in Koranna-Langeberg Mountain Bushveld (SVk15) (2 sites). A further 51 sites were in the Kalahari Duneveld Bioregion (SVkd) primarily in Gordonia Duneveld (SVkd1) (48 sites) but also Gordonia Kameeldoring Bushveld (SVkd2) (3 sites). In general, the dry northeast of the study area is dominated by open shrub / woodland on red sands of aeolian origin (SVk13) or grassland plus scattered shrubs and trees on plains of Namib sands (SVk16). The usually deep sands overlay calcrete, which outcrops in places making for stony soils, particularly towards the edge of the Nama Karoo. The arid northwest is dominated by a parallel dune system (SVkd1) with open shrubland in the dune valleys and grassland on the aeolian sands of the dune ridges. The dunes interdigitate into the Nama Karoo due to the prevailing northwest / southeast winds (Fig. 1).

A total of 303 study sites were in the Nama Karoo Biome as defined by Mucina & Rutherford (2006). These comprised 167 sites in the Bushmanland and West Griqualand Bioregion (NKb) primarily on two vegetation units, Bushmanland Arid Grassland (NKb3) (118 sites) and Bushmanland Basin Shrubland (NKb6) (34 sites), but also in Lower Gariep Brokenveld (NKb1) (7 sites) and Kalahari Karroid Shrubland (NKb5) (8 sites). A further 136 study sites were in the Upper Karoo Bioregion (NKu) primarily in Northern Upper Karoo (NKu3) (102 sites) and Eastern Upper Karoo vegetation units (NKu4) (33 sites) but also Northern Karoo Hardeveld (NKu2) (1 site). In general, the arid southwest of the study area is dominated by sparse grassland (Nkb3) or open scrub with sparse grass (NKb6) on clay loam top and subsoils (FAO 2012, USDA soil classification). The cooler, dry southeast uplands are dominated by open shrub / grassland (NKu3) or grassland with scattered shrubs (NKu4) on shallow or deep sandy clay loam or clay loam (FAO 2012, USDA soil classification). However, many saline pans of Azonal Inland Saline Vegetation (AZi) are scattered across the Upper Karoo (Mucina & Rutherford 2006) and these contain or, are fringed by loamy sand and, occasionally, lunate dunes all supporting grassland. About 20% of the sites in the Upper Karoo were placed in the proximity of pans on loamy sand.

Exceptionally, seven study sites were in other regions. These comprised two eastern sites in the Grassland Biome (Dry Highveld Grassland Bioregion (Gh), Bessemkaree Koppies shrubland vegetation unit (Gh4)). The remainder were in Azonal Vegetation (AZ), either Inland Saline Vegetation comprising Bushmanland Vloere (AZi5) clay pans (3 sites) or Upper Gariep Alluvial Vegetation (AZa4) comprising sands (2 sites) bordering the River Orange.

B.

An improved biogeographical database for Southern Africa has been constructed from locality records in Pretoria museums (Ditsong Museum, formerly Transvaal Museum; National Collection of Insects; reference collection of the University of Pretoria); from reliable published localities (Doube 1991, Davis 1996, Davis & Scholtz 2004, Davis et al. 1999, 2003, 2005, 2012, 2013, 2014, Jacobs et al. 2010, Tshikae et al. 2013 - see papers or supplementary files); and from unpublished field data from South Africa including that from the present study. These data are used in entirety to generate distribution maps within 17^oS x 32^oE map panels in a book on the conservation status of dung beetles in South Africa, Botswana and Namibia that is currently in preparation. The Pretoria museum databases will become available on the SANBI (South African National Biodiversity Institute) website when preparation and editing for errors is complete. The Pretoria museum data

for South Africa are currently being loaded onto the dedicated dung beetle section of the Virtual Museum website of the Animal Demography Unit at the University of Cape Town <http://vmus.adu.org.za/ >.

REFERENCES FOR PUBLISHED LOCALITIES

Davis ALV. 1996. Habitat associations in a South African, summer rainfall, dung beetle community (Coleoptera: Scarabaeidae, Aphodiidae, Staphylinidae, Histeridae, Hydrophilidae). *Pedobiologia* **40:** 260–280.

Davis ALV, Scholtz CH. 2004. Local and regional species ranges of a dung beetle assemblage from the semi-arid Karoo/Kalahari margins, South Africa. *Journal of Arid Environments* **57:** 61–85.

Davis ALV, Scholtz CH, Chown SL. 1999. Species turnover, community boundaries and biogeographical composition of dung beetle assemblages across an altitudinal gradient in South Africa. *Journal of Biogeography* **26:** 1039–1055.

Davis ALV, Scholtz CH, Deschodt C. 2005. A dung beetle survey of selected Gauteng nature reserves: implications for conservation of the provincial scarabaeine fauna. *African Entomology* **13:** 1–16.

Davis ALV, Scholtz CH, Swemmer AM. 2012. Effects of land usage on dung beetle assemblage structure: Kruger National Park versus adjacent farmland in South Africa. *Journal of Insect Conservation* **16:** 399–411.

Davis ALV, Swemmer AM, Scholtz CH, Deschodt CM, Tshikae BP. 2014. Roles of environmental variables and land usage as drivers of dung beetle assemblage structure in mopane woodland. *Austral Ecology* **39:** 313-327.

Davis ALV, Van Aarde RJ, Scholtz CH, Delport JH. 2003. Convergence between dung beetle assemblages of a post-mining vegetational chronosequence and unmined dune forest. *Restoration Ecology* **11:** 29–42.

Davis ALV, van Aarde RJ, Scholtz CH, Guldemond RAR, Fourie J, Deschodt CM. 2013. Is microclimate-driven turnover of dung beetle assemblage structure in regenerating coastal vegetation a precursor to re-establishment of a forest fauna? *Journal of Insect Conservation* **17:** 565–576.

Doube BM. 1991. Dung beetles of southern Africa. In: Hanski I, Cambefort Y, eds. *Dung beetle ecology*. Princeton: Princeton University Press, 133–155, 382–387.

Jacobs CT, Scholtz CH, Escobar F, Davis ALV. 2010. How might intensification of farming influence dung beetle diversity (Coleoptera: Scarabaeidae) in Maputo Special Reserve (Mozambique)? *Journal of Insect Conservation* **14:** 389–399.

Tshikae BP, Davis ALV, Scholtz CH. 2013. Dung beetle assemblage structure across the aridity and trophic resource gradient of the Botswana Kalahari: patterns and drivers at regional and local scales. *Journal of Insect Conservation* **17:** 623–636.

Table S2. Key to farms in Figure 1, year of sampling, and number of study sites.

_____

1. Massakloutjie (2003, 5)	23. Gordonsfontein (2008, 4)	45. Soetvlei (2009, 4)	67. Khaboom (2010, 4)
2. Florida (2003, 6)	24. Oppermansdam (2008, 4)	46. Retreat (2004, 6)	68. Middelka (2009, 4)
3. Oupashoop (2003, 6)	25. Raapfontein (2008, 4)	47. Redlands (2009, 4)	69. Bloubosdam (2010, 4)
4. Rooiwater (2005, 5)	26. Theefontein (2008, 4)	48. Grashoek (2004, 4)	70. Donkerdeel (2010, 4)
5. Geselskop (2005, 4)	27. Constantia (2008, 4)	49. Brakpoort (2004, 5)	71. Kalkwerfputs (2010, 4)
6. Kotzesrus (2003, 5)	28. Jagpoort (2007, 4)	50. Modderfontein 1 (2004, 6)	72. Brulpan 1 (2001, 2003;
7. Panvlei (2003, 6)	29. Dröefontein (2007, 4)	51. Grootfourieskolk (2011, 4)	9, 6)
8. Panheuwel (2004, 5)	30. Swartkoppies (2007, 4)	52. Voorspit (2011, 4)	73. Kraalkop (2004, 6)
9. Holkrans (2005, 5)	31. Spreeufontein (2007, 4)	53. Uitspanpan (2011, 4)	74. Koegrabie (2004, 7)
10. Rooikuile (2003, 6)	32. Lemoenkloof (2007, 4)	54. Kafferskolk (2009, 3)	75. Rooiput (2006, 4)
11. Bitterputs (2005, 5)	33. Westfront (2007, 4)	55. Mierdam (2009, 4)	76. Sonderpan (2006, 4)
12. Eland (2003, 6)	34. Donkerhoek (2011, 4)	56. Nelspoortjie (2006, 5)	77. Klipkoppies (2004, 4)
13. La Gratitude (2004, 6)	35. Witfontein (2007, 4)	57. Boesmansberg (2006, 5)	78. Eksteenkuil (2004, 6)
14. Swemkuil (2003, 7)	36. Kiewitskuil (2011, 4)	58. Platsambok (2009, 4)	79. Christiana (2004, 6)
15. Mooidraai (2006, 5)	37. Platkuil (2011, 4)	59. Buisvlei (2003, 7)	80. Leeukop (2004, 5)
16. Vlakpan (2005, 5)	38. Blomfontein (2007, 4)	60. Deelpan (2003, 6)	81. Driekop (2009, 4)
17. Herbou (2006, 4)	39. Renswoude (2007, 4)	61. Springputs (2005, 5)	82. Pypklip (2009, 4)
18. Taaibos (2005, 5)	40. Modderfontein 2 (2007, 4)	62. Draghoender (2010, 4)	83. Sonderhuis (2005, 4)
19. Karsonaatjieskraal (2008, 4)	41. Bloemhof (2008, 4)	63. Brulpan 2 (2010, 4)	84. Maniertydskolk (2005, 4)
20. Somerlus (2008, 4)	42. Eufasia (2008, 4)	64. Mariba (2005, 5)	85. Boomrivier (2009, 4)
21. Brulfontein (2008, 4)	43. Middelfontein (2008, 4)	65. Tarkaskop (2009, 4)	86. Opdam (2005, 4)
22. Swagersfontein (2008, 4)	44. Biega (2009, 4)	66. Brierspan (2009, 4)	87. Taaibosdam (2005, 4)

_____

One 48 h sampling occasion from each farm, mostly during March of specified year except Brulpan (1) (two 48 h samples). Study sites per farm vary in number according to size of property and degree of habitat variation.

Table S3. List of 127 scarabaeine dung beetle species (four in footnotes*) recorded during a 10 year survey of 412 study sites in the Northern Cape and their abundances in five regions defined by ordination (averages multiplied by 100 to assist interpretation) (see footnotes for keys to diel flight and functional groups).

SPECIES (and functional classification)^^	Dry wt (mg) Diel activity^^	Gariep Karoo Factor 1	Kalahari Factor 2	Bushman -land Factor 3	Upper Karoo Factor 4	Gariep Stony Factor 5
Canthonini		Mean / trap / day x100				
1. *Epirinus aeneus* Wiedemann (B)	12.9 D	50.8	0.2	2.6	0.0	3.5
2. *Epirinus flagellatus* (Fabricius) (B)	29.9 D	0.0	0.0	0.0	0.3	0.0
3. *Epirinus striatus* Scholtz & Howden (B)	17.1 D	81.2	0.0	0.0	300.0	0.0
4. *Odontoloma* sp. (?K)	0.8^D	6.8	0.0	0.0	140.2	0.0
5. *Pycnopanelus krikkeni* Cambefort (?K)	2.5 D	48.4	7.2	537.3	0.0	26.8
Scarabaeini						
6. *Pachylomera opaca* van Lansberge (B)	461.1 D	0.6	89.1	0.9	0.0	0.5
7. *Pachylomera femoralis* (Kirby) (B)	1294.3 D	0.0	83.2	0.0	0.0	0.0
8. *Scarabaeus* (*Kheper*) *kalaharicus* Davis, Deschodt, Scholtz(B)	650.0^D	0.0	0.2	0.0	0.0	0.0
9. *Scarabaeus* (*Kheper*) *lamarcki* Macleay (B)	770.4 D	0.0	6.7	0.0	0.0	0.0
10. *Scarabaeus* (*Kheper*) *prodigiosus* (Erichson) (B)	800.0^N	0.0	0.2	0.0	0.0	0.0
11. *Scarabaeus* (*Scarabaeolus*) *bohemani* Harold (B)	44.0 D	469.4	32.1	569.0	145.1	140.8
12. *Scarabaeus* (*Scarabaeolus*) *anderseni* Waterhouse (B)	30.0^D	0.0	6.0	0.2	0.0	0.0
13. *Scarabaeus* (*Scarabaeolus*) *damarensis* Janssens (B)	51.1 D	2.1	2123.9	0.0	0.0	0.0
14. *Scarabaeus* (*Scarabaeolus*) *flavicornis* (Boheman) (B)	104.8 D	4.3	121.0	2.8	0.0	1.0
15. *Scarabaeus* (*Scarabaeolus*) *fritschi* (Harold) (B)	157.7 D	86.1	5.6	0.2	0.0	0.5
16. *Scarabaeus* (*Scarabaeolus*) *inoportunus* Ferreira (B)	59.5 D	0.0	397.9	26.1	0.0	0.0
17. *Scarabaeus* (*Scarabaeolus*) *inquisitus* Péringuey (B)	67.4 D	0.5	4.2	0.0	0.3	0.0
18. *Scarabaeus* (*Scarabaeolus*) *karrooensis* zur Strassen (B)	44.0^D	17.4	3.0	108.5	0.0	17.3
19. *Scarabaeus* (*Scarabaeolus*) *kochi* Ferreira (B)	49.7 D	3.9	42.3	0.0	0.3	0.0
20. *Scarabaeus* (*Scarabaeolus*) *megaparvulus* Davis, Deschodt (B)	53.4 D	23.3	0.0	0.0	9.2	1.0
21. *Scarabaeus* (*Scarabaeolus*) *pabulator* Péringuey (B)	43.6 D	0.8	0.7	71.6	0.0	0.0
22. *Scarabaeus* (*Scarabaeolus*) *parvulus* (Boheman) (B)	15.0 D	60.9	102.3	44.1	0.7	12.1
23. *Scarabaeus* (*Scarabaeus*) *basuto* zur Strassen (B)	159.8 D	98.3	0.0	0.0	193.5	0.0
24. *Scarabaeus* (*Scarabaeus*) *costatus* (Wiedemann) (B)	151.3 D	0.6	517.6	3.3	0.0	0.0
25. *Scarabaeus* (*Scarabaeus*) *vicinus* Janssens (B)	431.2 D	31.0	6.0	0.0	24.8	0.0
26. *Scarabaeus* (*Scarabaeus*) *proboscideus* (Guérin-Meneville)(B)	548.9 N	1.3	569.1	55.9	0.0	5.1
27. *Scarabaeus* (*Scarabaeus*) *satyrus* (Boheman) (B)	281.9 N	101.6	72.6	325.4	20.6	49.5
28. *Scarabaeus* (*Scarabaeus*) *viator* Péringuey (B)	302.5 D	2183.9	69.1	0.7	2540.8	38.9
29. *Scarabaeus* (*Scarabaeus*) *zambesianus* Péringuey (B)	388.4 N	0.0	116.7	0.0	0.0	0.0
Gymnopleurini						
30. *Allogymnopleurus thalassinus* (Klug) (B)	42.6 D	524.5	1211.0	57.7	9.2	281.3
31. *Gymnopleurus aenescens* Wiedemann (B)	29.9 D	6.8	57.5	6.3	0.0	41.4
32. *Gymnopleurus andreaei* Ferreira (B)	43.7 D	43.6	68.1	440.6	0.0	30.8
33. *Gymnopleurus asperrimus* (Felsche) (B)	30.1 D	482.6	636.6	1278.9	0.7	56.6
34. *Gymnopleurus humanus* Macleay (B)	28.9 D	2142.1	939.3	5520.4	519.0	2582.3
35. *Gymnopleurus leei* (Fabricius) (B)	56.5 D	0.2	0.0	0.0	79.4	0.5
Sisyphini						
36. *Neosisyphus kuehni* (Haaf)** (B)	46.8 D	0.0	0.0	0.0	1.0	0.0
37. *Neosisyphus macrorubrus* (Paschalidis) (B)	28.8 D	41.4	29.6	0.0	190.5	8.1
Ateuchini						
38. *Pedaria* sp. (K)	12.4 N	0.2	120.6	3.1	0.0	3.5
39. *Pedaria picea* Fahraeus (K)	13.5 N	0.0	0.3	0.0	0.0	0.0
Coprini						
40. *Catharsius calaharicus* Kolbe (T)	419.6 N	0.7	49.0	0.0	0.0	1.5
41. *Catharsius melancholicus* Boheman (T)	532.0 N	0.0	0.2	0.0	0.0	0.0
42. *Catharsius pandion* Harold** (T)	404.6 N	0.0	0.2	0.0	0.0	0.0
43. *Catharsius tricornutus* Degeer (T)	283.1 N	0.0	0.2	0.0	0.0	0.0
44. *Catharsius vitulus* Boheman (T)	365.1 N	0.6	0.0	0.0	41.8	0.0
45. *Copris antares* Ferreira (T)	120.0^N	0.0	0.0	0.0	0.3	0.0
46. *Copris cassius* Péringuey (T)	63.3 N	0.0	21.7	0.0	0.0	0.0
47. *Copris cornifrons* Boheman (T)	114.6 N	0.0	3.1	0.0	0.0	0.0
48. *Copris elphenor* Klug (T)	352.5 N	0.0	3.2	0.0	0.0	0.0
49. *Copris inhalatus* Quedenfeldt ssp *perturbator* Péringuey (T)	220.0^N	0.0	0.2	0.0	0.0	0.0
50. *Heliocopris faunus* Boheman (T)	1170.8 N	8.3	0.0	0.2	9.5	0.0
51. *Heliocopris hamadryas* (Fabricius) (T)	1500.0^N	0.2	0.0	0.0	0.0	0.0
52. *Metacatharsius anderseni* (Waterhouse) (T)	51.1 N	0.0	43.1	0.0	0.0	0.0
53. *Metacatharsius dentinum* Ferreira (T)	14.1 N	5.8	23.0	14.3	0.7	1.0
54. *Metacatharsius exiguus* (Boheman) (T)	70.0^N	0.0	0.2	0.0	0.0	0.0
55. *Metacatharsius exiguiformis* Ferreira (T)	23.5 N	0.5	2992.2	62.7	0.0	2.0
56. *Metacatharsius latifrons* (Harold) (T)	71.8 N	0.0	13.7	0.0	0.0	0.0
57. *Metacatharsius marani* Balthasar (T)	72.2 N	1173.2	250.7	1363.1	37.6	263.6
58. *Metacatharsius pumilioniformis* Ferreira (T)	14.0^N	0.2	124.0	0.0	0.0	0.0
59. *Metacatharsius troglodytes* (Boheman) (T)	66.4 N	0.0	61.3	0.0	0.0	0.0

^Estimated dry wt. ^^Diel activity: D = Day, N = Night. Functional group: B = Ball roller, T = Tunneler, K = Kleptocoprid, E = Endocoprid.

SPECIES (and functional classification)^^	Dry wt (mg) Diel activity^^	Gariep Karoo Factor 1	Kalahari Factor 2	Bushman -land Factor 3	Upper Karoo Factor 4	Gariep Stony Factor 5
Onitini						
60. *Cheironitis audens* Péringuey (T)	89.1 D	24.4	0.2	17.6	32.7	7.1
61. *Cheironitis hoplosternus* Harold (T)	62.3 D	10.5	66.3	0.2	41.5	18.2
62. *Cheironitis scabrosus* (Fabricius) (T)	47.5 D	254.8	21.2	97.9	662.7	290.4
63. *Cheironitis* sp. (T)	60.9 D	7.1	5.4	14.6	0.0	8.1
64. *Onitis alexis* Klug (T)	102.6 N	0.4	1.0	0.7	0.0	1.5
65. *Onitis aygulus* (Fabricius) (T)	183.4 N	1.0	4.9	1.4	2.3	1.0
66. *Onitis caffer* Boheman (T)	198.0 N	0.0	0.0	0.0	0.7	0.0
67. *Onitis confusus* Boheman (T)	220.0 N	0.0	0.0	0.0	2.3	0.0
68. *Onitis deceptor* Péringuey (T)	366.0 N	0.0	1.6	0.0	0.0	0.0
Onthophagini						
69. *Caccobius cavatus* d'Orbigny (?K)	1.0^N	0.0	1.0	0.0	0.0	0.0
70. *Caccobius ferrugineus* Fahraeus (K)	3.9 N	0.0	24.2	0.0	0.0	0.0
71. *Caccobius nigritulus* Klug (K)	2.8 D	0.2	29.4	0.0	0.0	0.0
72. *Cleptocaccobius viridicollis* (Fahraeus) (K)	0.9 N	1.0	5.4	0.0	40.5	0.0
73. *Digitonthophagus gazella* (Fabricius)** (T)	24.2 N	47.8	11.6	100.0	1.0	36.9
74. *Euonthophagus flavimargo* (d'Orbigny) (T)	7.8 N	23.1	263.8	8.0	0.0	73.7
75. *Euonthophagus vicarius* Péringuey** (T)	20.0 N	112.3	0.2	0.0	153.9	0.5
76. *Hyalonthophagus* sp. (T)	14.0 D	37.4	3.3	0.0	0.0	1.0
77. *Onthophagus acutus* d'Orbigny (T)	25.0^N	0.4	0.5	0.0	0.0	0.0
78. *Onthophagus aeruginosus* Roth (T)	9.2 D	0.0	0.0	0.0	0.0	71.2
79. *Onthophagus albipennis* Péringuey (K)	5.2 D	1739.1	44.4	1.2	204.2	36.4
80. *Onthophagus* sp. nr *albipennis* (?)	2.9 ?	0.4	0.0	0.0	0.0	0.0
81. *Onthophagus binodis* Thunberg (T)	45.0^D	0.0	0.0	0.0	0.3	0.0
82. *Onthophagus bovinus* Péringuey (T)	25.0^D	0.7	0.0	0.2	0.0	0.5
83. *Onthophagus cameloides* d'Orbigny (T)	40.6 D	2.7	0.0	0.2	7.2	0.0
84. *Onthophagus convexus* d'Orbigny (K)	1.0 D	37.9	716.7	120.9	3.6	41.9
85. *Onthophagus* sp. nr *cribripennis* (T)	15.0^D	0.1	0.3	0.0	0.0	0.0
86. *Onthophagus cyaneoniger* d'Orbigny (T)	3.0^D	0.0	0.0	0.0	255.6	0.0
87. *Onthophagus depressus* Harold (T)	24.9 N	0.0	0.0	0.0	0.0	0.5
88. *Onthophagus fritschi* d'Orbigny (?T)	7.0 D	12.1	0.0	0.0	464.4	529.8
89. *Onthophagus granulifer* Harold (T)	4.7 D	0.4	3214.7	6.6	0.0	5.1
90. *Onthophagus impressicollis* Boheman (?T)	15.0^D	0.0	2.8	0.0	0.0	0.0
91. *Onthophagus* sp. nr *lugubris* (T)	17.6 D	0.2	0.0	0.0	10.5	0.0
92. *Onthophagus pallidipennnis* Fahraeus (K)	6.1 D	0.0	33.8	0.0	0.0	0.0
93. *Onthophagus probus* Péringuey (K)	1.9 D	861.4	3327.3	1019.7	0.0	311.6
94. *Onthophagus* sp. nr *probus* (K)	1.0 D	0.0	2722.1	0.7	0.0	1.0
95. *Onthophagus pugionatus* Fahraeus (T)						
96. *Onthophagus quadraticeps* Harold (T)	13.2 N	0.0	591.8	1.9	0.0	1.0
97. *Onthophagus rasipennis* d'Orbigny (K)	3.4 N	0.0	0.2	0.0	0.0	0.0
98. *Onthophagus stellio* Erichson** (?T)	2.2 N	27.1	9037.7	4.2	0.0	121.7
99. *Onthophagus signatus* Fahraeus (K)	5.1 D	1235.6	6311.9	479.8	9.8	1209.6
100. *Onthophagus semiflavus* Boheman (K)	3.8 D	7.2	84.1	61.5	0.0	0.0
101. *Onthophagus* sp. nr *sugillatus* (?T)	3.2 D	0.1	0.0	0.0	1.6	0.5
102. *Onthophagus suturalis* Péringuey** (K)	7.6 D	483.5	0.5	8.7	633.7	17.7
103. *Onthophagus verticalis* Fahraeus (K)	7.8 N	0.0	1.1	0.0	0.0	0.0
104. *Onthophagus vinctus* Erichson (?T)	5.8 N	0.0	1.3	0.0	0.0	2.5
105. *Onthophagus* sp. A (?K)	2.8 ?	1.6	57.2	1.4	0.0	2.5
106. *Onthophagus* sp. B (?K)	2.1 ?	4.1	26.3	0.0	0.0	0.0
107. *Onthophagus* sp. C (?)	4.5^?	0.0	0.0	0.0	0.0	0.5
108. *Onthophagus* sp. D (?)	2.5^?	0.1	0.0	0.0	0.3	0.0
109. *Onthophagus* sp. E (?)	1.0^?	0.1	12.7	0.0	0.0	0.0
110. *Onthophagus* sp. F (?)	2.5^?	0.1	0.0	0.0	0.0	1.0
111. *Onthophagus* sp. G (T)	3.1 ?	457.9	546.2	219.5	95.4	2767.2
112. *Phalops bubalus* (Harold) (T)	23.6 D	0.0	0.0	0.0	220.9	0.0
113. *Phalops dregei* Harold (T)	28.2 D	119.6	14.7	0.0	317.0	53.0
114. *Phalops wittei* Harold (T)	37.5 D	60.1	258.1	32.4	0.0	30.3
115. *Phalops pyroides* d'Orbigny (T)	33.0 D	24.5	11.9	7.0	1.3	60.1
116. *Phalops rufosignatus* van Lansberge (T)	26.8 D	126.8	256.2	9.2	114.4	123.7
117. *Proagoderus lanista* (Castelnau) (T)	55.0^D	0.0	0.0	0.0	5.6	0.0
118. *Proagoderus sapphirinus* (Fahraeus)** (T)	38.5 D	0.0	301.1	0.0	0.0	0.0
Oniticellini						
119. *Drepanocerus patrizii* (Boucomont) (?E)	5.3 D	0.0	0.2	0.0	3.6	0.0
120. *Euoniticellus africanus* (Harold) (T)	27.2 D	4.2	0.2	0.0	421.6	0.0
121. *Euoniticellus intermedius* (Reiche) (T)	11.8 D	27.9	52.3	9.4	72.9	67.2
122. *Euoniticellus triangulatus* (Harold) (T)	10.0^D	0.4	0.0	0.0	0.3	0.0
123. *Oniticellus formosus* Chevrolat (E)	13.3 D	0.0	1.6	0.0	0.0	0.5

*Species recorded at unclassified study sites: *Metacatharsius* sp., *Onthophagus* sp. H, *Onthophagus* sp. I, *Eodrepanus fastiditus* (Péringuey). **Species names requiring revision.