



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

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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 km² 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 ('Gariiep Karoo', 'Gariiep Stony Karoo') showed no dominance. Biogeographically, endemism dominates the Northern Cape transition zone: south-west arid groups in Nama Karoo regions; Kalahari plus north-east 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. © 2016 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2016, **119**, 329–347.

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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, Cerda & Retana, 2014) that result from interaction between abiotic environmental drivers such as climate (temperature/rainfall) (Hawkins *et al.*, 2003; Carnicer & Díaz-Delgado, 2008),

topography (Davis, Scholtz & Chown, 1999; Hodkinson, 2005) or edaphic character (Tuomisto, Zuquim & Cárdenas, 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, Scholtz & Deschodt, 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.

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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 south-east (Upper Karoo and Highveld; collectively the Drakensberg uplift zone), leading to erosion and sand deposition in the north-west (Kalahari Basin), followed by Pliocene/Pleistocene aridification that was most intense in the south-west (Bushmanland) (Dauteuil, Bessin & Guillocheau, 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 south-west coast of Africa (Marlow *et al.*, 2000) caused the seasonal north-east 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 south-west 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 south-west expansion of the easterly winds only reaches the Northern Cape in late summer. Hence the increasing aridity from the Kalahari into Bushmanland south-westwards 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 south-west 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, Davis & Scholtz, 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 mg to > 2000 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, Davis & Scholtz, 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 south-west/north-east 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 south-west and south-east comprise winter or bimodal spring/autumn climates 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 south-west and Nama Karoo in the more late summer rainfall-influenced north-east. Further north-east, the moist, mid-summer rainfall climate supports the Indian Ocean Coastal Biome on the east coast; the Grassland Biome in higher altitude, south-east areas; and the Savanna Biome in the remaining areas.

The study area of 50 200 km² 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 north-west and north-east 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 south-west and south-east 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 Supporting Information (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, as 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 to 12 farms per year (Supporting Information, Table S2) and from 1 to 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 c. 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

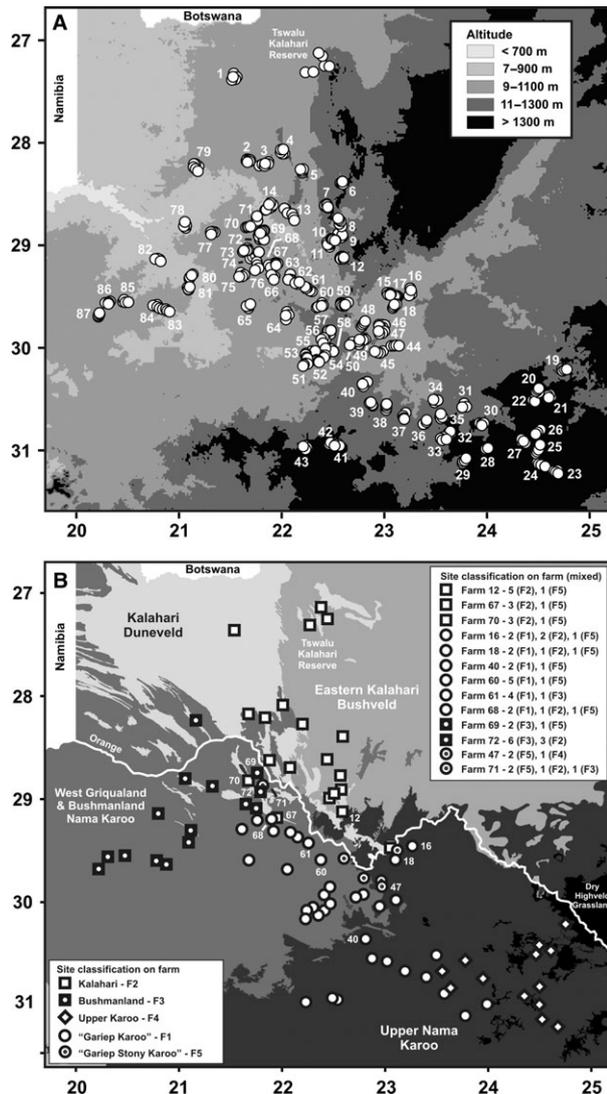


Figure 1. The Northern Cape study area, South Africa. A, Location of 412 study sites on 87 farms and one private reserve (key to farms: Supporting Information, Table S2). B, Regional classification of 87 farms (single data points) and one private reserve (three data points) (see Fig. 3) plotted on a basemap of floral bioregions (Mucina & Rutherford, 2006).

at ground level above a trap using two strong wires. At each site, 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 ($1 \times 1 \text{ km}^2$ polygons), annual temperature (max. + min./2) ($5 \times 5 \text{ km}^2$ 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 vs. 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 south-west and moist, warm temperate, summer rainfall climate (II) in the north-east. Climatic distribution data were determined for 113 out of 127 recorded species using an unpublished database (Supporting Information, 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 Inc., 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 Inc., 2015 – Statistica v.12). A data matrix was constructed comprising mean abundance/site/day at 412 study sites for 127

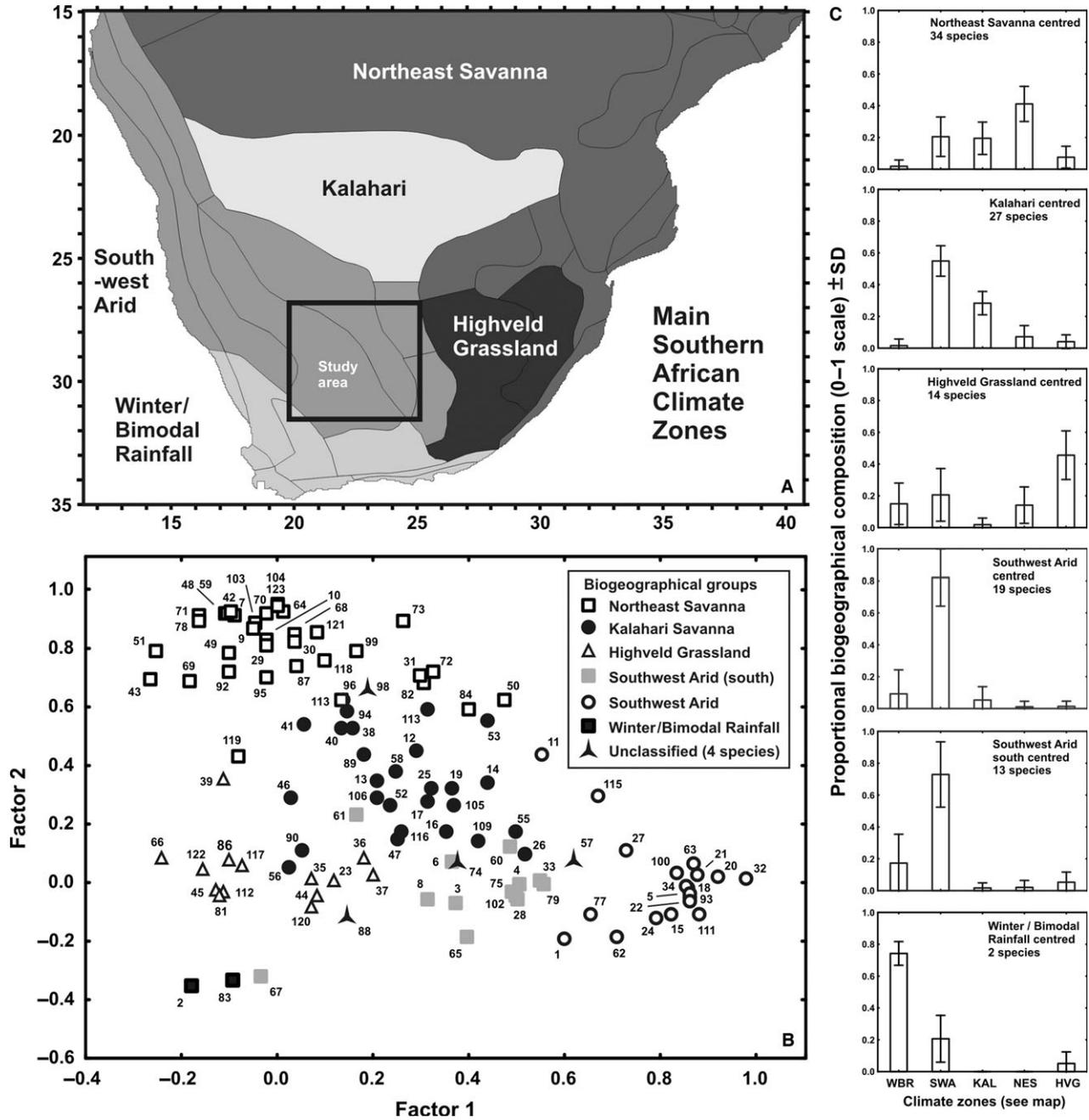


Figure 2. A, Main climatic regions of southern Africa (modified from Walter & Lieth, 1964). B, Ordination plot showing distances between the southern African climatic distributions of 113 taxa from the Northern Cape species pool of 127 species (see Supporting Information, Table S3 for key). C, Bar diagrams showing mean proportional climatic bias in six biogeographical species groups [0–1 scale; WBR, winter/Bimodal Rainfall; SWA, south-west arid; SWS, south-west arid (south); KAL, Kalahari; NES, northeast savanna; HVG, Highveld Grassland].

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 their

descriptive statistics were generated using the same procedure as in the biogeographical analysis. General Linear Model (GLM) one-way analyses of variance (ANOVAs) were used to determine the strength of separation in ordinal space both between clusters and along each factor.

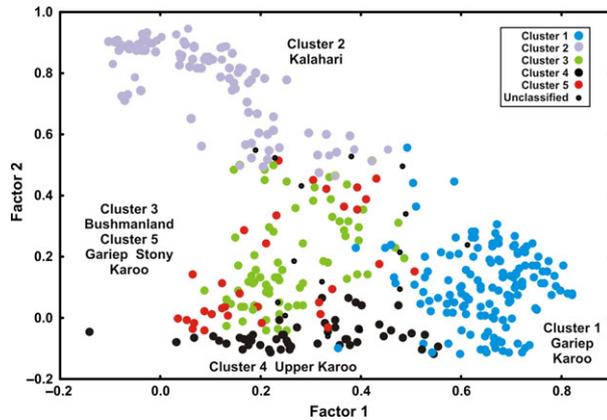


Figure 3. Ordination plot showing the distance between dung beetle assemblage structure at 412 study sites in the Northern Cape with classification into five regional clusters.

Significant environmental differences between dung beetle regions and principal drivers of faunal differences were determined using General Linear and Regression Models (Statsoft Inc., 2015 – Statistica v.12). GLM one-way ANOVAs and Tukey's honest significant difference (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 Inc., 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 \times 94 species (Kalahari), 71 sites \times 51 species (Bushmanland), 51 sites \times 53 species (Upper Karoo) and 32 sites \times 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 ($\exp H'$) for each study site. The means of the values for numbers of species and $\exp H'$ per site were calculated 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 Northern 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 Inc., 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, Laval & Schneider, 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 (Clarke & Gorley, 2001).

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, South-west Arid (south), and winter/Bimodal Rainfall. Shared variance represented by secondary factor S1 showed that there was appreciable overlap between the two south-west arid species groups and the Kalahari group (Table 1). There was also appreciable overlap (S2) between the north-east 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%).

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 and 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 south-west 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 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).

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

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 South-west
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	South-west Arid
P2	0	0.27	0	0	0	0	North-east 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); '0', no correlation at six places of decimals; sum of r^2 occasionally > 1 due to rounding up.

*Proportional variance derived from eigenvalues.

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.

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 vs. finer-grained soils and stony vs. deep soils defined by categorical on-site observations supports the differences between study sites (Table 6).

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 south-east 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,

Table 2. Mean (\pm SD) 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

Rows	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5	F value (d.f.)
(A)						
Factor 1	0.651 \pm 0.089 ^a	0.101 \pm 0.121 ^d	0.274 \pm 0.140 ^b	0.281 \pm 0.147 ^b	0.221 \pm 0.189 ^c	294.33*** (4, 685)
Factor 2	0.104 \pm 0.137 ^b	0.770 \pm 0.139 ^a	0.136 \pm 0.159 ^b	-0.031 \pm 0.061 ^c	0.144 \pm 0.185 ^b	492.43*** (4, 505)
Factor 3	0.257 \pm 0.092 ^b	0.181 \pm 0.148 ^c	0.748 \pm 0.133 ^a	0.047 \pm 0.087 ^d	0.233 \pm 0.158 ^{bc}	317.40*** (4, 345)
Factor 4	0.295 \pm 0.145 ^b	-0.056 \pm 0.045 ^e	0.053 \pm 0.070 ^d	0.760 \pm 0.104 ^a	0.125 \pm 0.139 ^c	449.74*** (4, 250)
Factor 5	0.230 \pm 0.137 ^c	0.158 \pm 0.180 ^c	0.347 \pm 0.114 ^b	0.197 \pm 0.151 ^c	0.593 \pm 0.089 ^a	51.94*** (4, 155)
(B)						
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***	47.92***	
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).

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); ‘0’, no correlation at six places of decimals; sum of r^2 occasionally > 1 due to rounding up.

*Proportional variance derived from eigenvalues.

Table 4. Mean environmental data \pm SD 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) (°C) [†]	Soil composition (% sand grains) [†]	Northern Cape region
Cluster 1	1110.0 \pm 111.0 ^b	190.8 \pm 28.9 ^b	17.6 \pm 1.4 ^c	47.8 \pm 14.9 ^b	Gariep Karoo
Cluster 2	1053.0 \pm 84.5 ^c	194.8 \pm 30.3 ^b	19.2 \pm 0.5 ^a	82.8 \pm 16.4 ^a	Kalahari
Cluster 3	924.8 \pm 79.2 ^d	140.9 \pm 22.5 ^c	19.3 \pm 0.7 ^a	50.1 \pm 19.8 ^b	Bushmanland Karoo
Cluster 4	1330.7 \pm 98.4 ^a	280.7 \pm 26.6 ^a	15.2 \pm 0.9 ^d	47.1 \pm 5.3 ^b	Upper Karoo
Cluster 5	1058.8 \pm 96.6 ^c	193.9 \pm 22.0 ^b	18.6 \pm 0.4 ^b	50.4 \pm 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).

moister sites to the north-east of the region (Cluster H) and lower appreciably drier sites to the south-west (Cluster G – Farms 77, 78, 80–87). The two Upper Karoo sub-regions comprised lower warmer sites to the west/north-west of the region (cluster I) and higher cooler sites to the east/south-east (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

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)]. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

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

Cluster	% Sand		Total <i>N</i> sites
	(average per site)	% Stony 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

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 moister but stony conditions within the Gariep Karoo.

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 (Supporting Information, 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).

The 60 most abundant species comprised from 98.3–99.7% 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 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.

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 (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; in each column, values followed by a different letter differed significantly at $P < 0.05$, Tukey’s HSD)

	(a) Coeff. of determ. (r^2)				(b) Mean environmental factors \pm SD				
	S1	P1	P2	P3	Altitude m	Rainfall mm	Temp. °C	% Sand	% Stony
Gariiep Karoo 138 samples (7 unclassified)									
Cluster A	0.70	0.30	0	0	1058.5 \pm 59.0 ^b	180.7 \pm 20.5 ^b	18.2 \pm 0.8 ^a	49.2 \pm 15.8	26.1
Cluster B	0.72	0	0.28	0	1256.9 \pm 86.1 ^a	243.2 \pm 24.4 ^a	15.4 \pm 0.9 ^c	49.6 \pm 13.2	22.2
Cluster C	0.79	0	0	0.21	1205.1 \pm 133.8 ^a	188.1 \pm 15.0 ^b	16.8 \pm 1.6 ^b	43.0 \pm 12.9	71.4
$F_{(df\ 2, 128)}$					65.78***	71.47***	65.07***	1.55	
Kalahari 102 samples (2 unclassified)									
Cluster D	0.74	0.26	0	0	1070.6 \pm 86.0 ^a	199.8 \pm 30.9 ^a	19.2 \pm 0.5 ^a	90.3 \pm 2.8 ^a	1.8
Cluster E	0.80	0	0.20	0	1042.1 \pm 97.0 ^{ab}	192.7 \pm 30.0 ^{ab}	19.3 \pm 0.6 ^a	70.9 \pm 23.3 ^b	52.0
Cluster F	0.72	0	0	0.28	1013.1 \pm 31.5 ^b	179.7 \pm 20.9 ^b	18.9 \pm 0.2 ^b	75.1 \pm 17.6 ^b	5.9
$F_{(df\ 2, 97)}$					3.49*	3.15*	4.20**	20.23***	
Bushmanland 71 samples (1 unclassified)									
Cluster G	0.80	0.20	0		885.8 \pm 71.4	126.7 \pm 16.7	19.4 \pm 0.7	45.0 \pm 14.7	33.3
Cluster H	0.80	0	0.20		984.3 \pm 49.2	162.0 \pm 22.8	19.0 \pm 0.7	56.2 \pm 19.4	57.1
$t_{(df\ 68)}$					6.36*	9.97**	2.76	2.46**	
Upper Karoo 51 samples									
Cluster I	0.75	0.25	0		1388.5 \pm 46.4	289.0 \pm 17.8	14.7 \pm 0.4	48.3 \pm 5.0	62.5
Cluster J	0.75	0	0.25		1233.4 \pm 85.0	266.8 \pm 33.2	16.0 \pm 0.9	45.2 \pm 5.5	68.4
$t_{(df\ 49)}$					8.44**	3.12**	7.19***	2.07	
Gariiep Stony Karoo 32 samples									
Cluster K	0.70	0.30	0		1059.1 \pm 95.6	197.5 \pm 19.6	18.6 \pm 0.3	49.9 \pm 13.5	80.0
Cluster L	0.70	0	0.30		1042.3 \pm 101.6	187.7 \pm 25.3	18.7 \pm 0.6	51.3 \pm 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); ‘0’, no correlation at six places of decimals.

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 (Gariiep Karoo, Gariiep Stony Karoo). Along the minimum spanning tree (Fig. 6), the 26 species of Pattern A showed from 46–100% of abundance on the deep

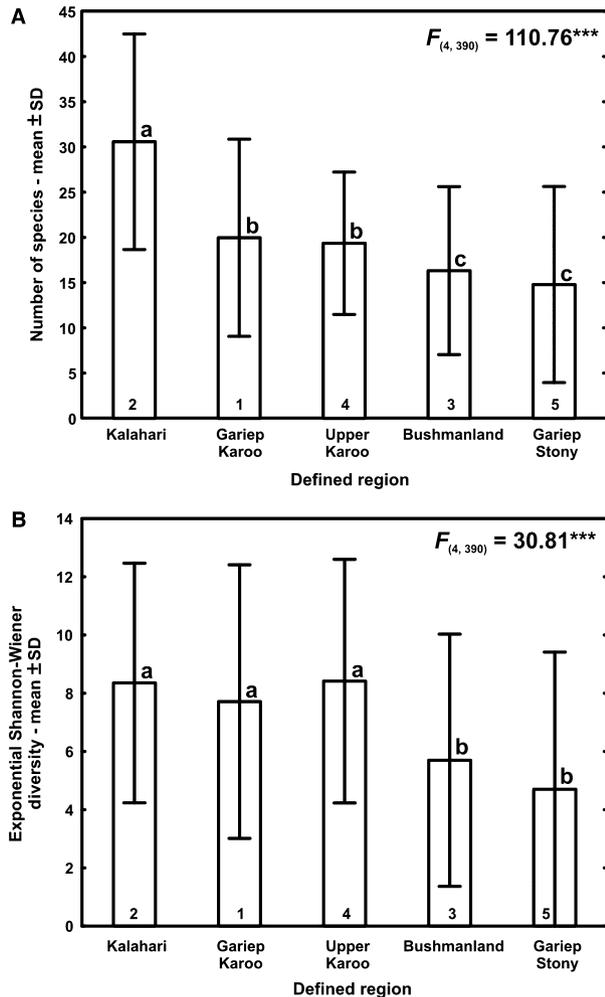


Figure 4. Mean number of dung beetle species (A) and mean exponential Shannon–Wiener diversity ($\exp H'$) (B) per study site in each of five Northern Cape regions [results for GLM one-way ANOVAs are inset ($***P < 0.001$); columns identified by a different letter differ significantly ($P < 0.05$, Tukey's HSD)].

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

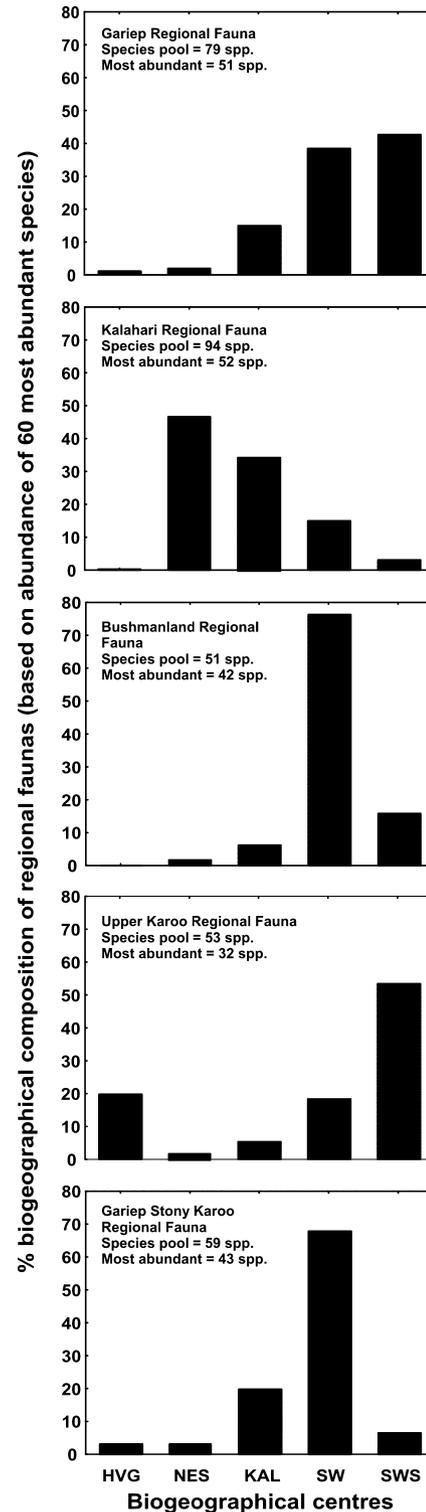


Figure 5. Proportional biogeographical composition within species assemblages of five regions across the Northern Cape transition zone derived from data for the 60 most abundant species (SW, south-west arid; SWS, south-west arid (south); KAL, Kalahari; NES, northeast savanna; HVG, Highveld Grassland).

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 tunnelling 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.

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, Hortal & Cabrerero-Sañudo, 2006; Mykrä & Muotka, 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, Dupont & Wefer, 2015) and fossil foraminifera (Diekmann, Fälker & Kuhn, 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 south-west (Deacon,

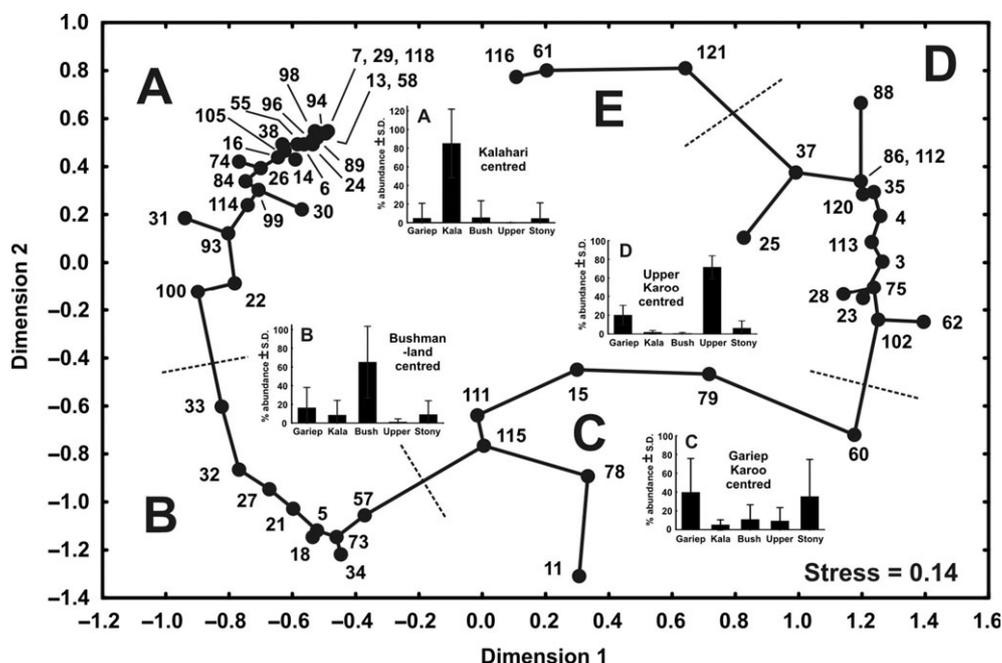


Figure 6. MDS ordination plot for the 60 most abundant species (99.1% total abundance) showing the distances between their abundance patterns across five Northern Cape regions. Patterns of similarity are supported by a minimum spanning tree along which three clusters and two scattered groups of species have been defined (key to species: Supporting Information, Table S3). Bar diagrams for clusters and species groups show mean percentage abundance across Northern Cape regions.

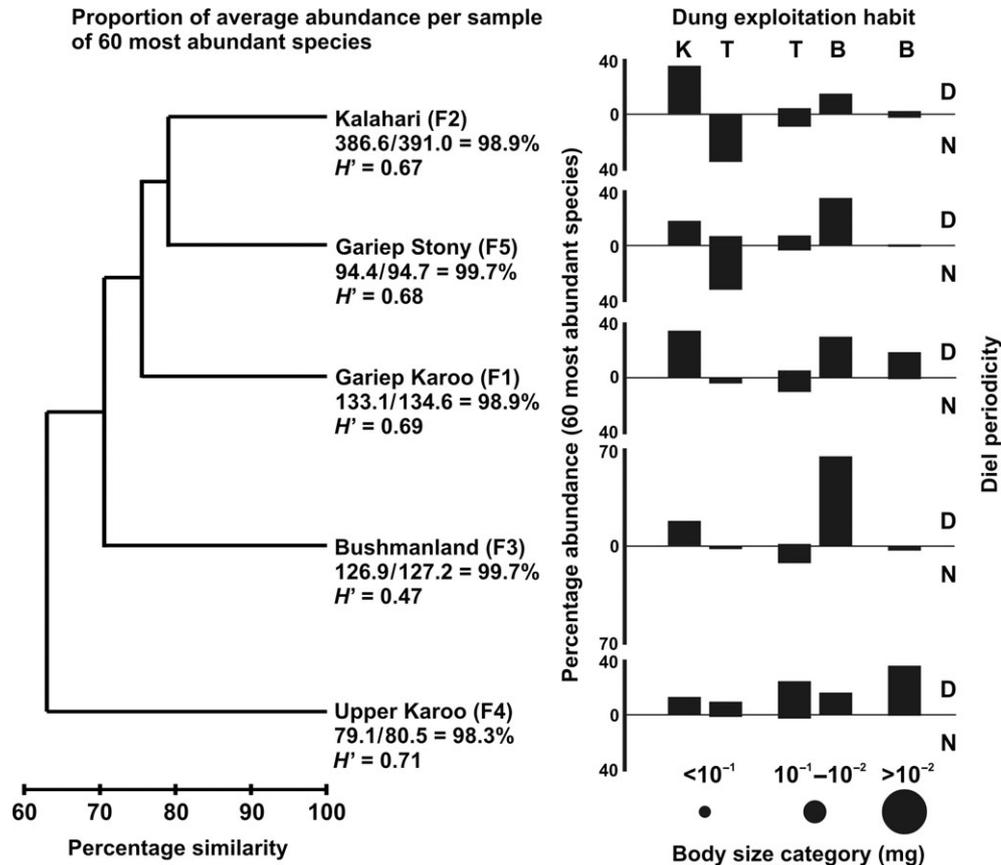


Figure 7. Patterns of functional structure in dung beetle assemblages of five Northern Cape regions. Bar diagrams are based on proportional abundance of the 60 most abundant species with axes comprising three body size classes ($< 10^{-1}$ to $> 10^{-2}$ mg, spots represent: 10^{-1} , 10^{-2} , 10^{-3} 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').

1983) that is perhaps partly reflected by low representation of subtropical/tropical C_4 grasses in the south-west (Dupont *et al.*, 2013) and north/south differences in sedimentary carbon accumulation along the south-west marine upwelling zone (Giraudeau, Meyers & Christensen, 2002). The current observable south-west/north-east 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 Myr 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 south-west arid centres, both climatic and edaphic drivers would be

responsible for endemism biased to the arid south-west edge of the Kalahari Basin. The division of south-west arid endemics into pan-south-west-centred and south-centred species groups reflects warmer, dryer vs. cooler, moister climate in uplifted areas. Cooler areas of the Upper Nama Karoo near the Grassland biome also include highveld elements. Elements of the north-east, 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 south-west 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 south-west 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, Sole & Scholtz, 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 Gariiep 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.*, 2013). 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 south-west 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 north-east/south-west trend in climate and edaphic character that developed in the Pliocene. Although the study area was entirely situated within the south-west arid, late summer rainfall region, only the Nama Karoo regions were dominated by south-west arid centred species. These regions differed in relative dominance between groups with widespread or southern bias in distribution according to warmer (Bushmanland, Gariiep Stony Karoo), intermediate (Gariiep Karoo) or cooler climate (Upper Karoo). The deep sands of the Kalahari savanna differed radically through dominance by north-east savanna and Kalahari-centred groups with a small widespread south-west arid component. The Kalahari group component decreased into the Nama Karoo where soils were less frequently sandy with similar rain but cooler conditions (Gariiep 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 north-east/south-west trend in climate and edaphic character. Numbers of species declined significantly from the deep sands of the south-west Kalahari to the cooler, less sandy conditions of the Gariiep 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 Gariiep 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, Lattke & Viloría, 2013; Tshikae, Davis & Scholtz, 2013c) although there are exceptions possibly related to asymmetric variability and interaction between factors such as aridity, soil type and/or temperature (Pfeiffer, Chimedregzen & Ulykpan, 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 south-west 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 south-west and increases to the moister north-east 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 *et 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 *et al.*, 2008) but now comprise the western end of a region defined as 'Gariiep Karoo'. This straddles the boundary between the Bushmanland and Upper Karoo floral bioregions (Mucina & Rutherford, 2006). The Gariiep 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 & Rutherford (2006).

CONCLUSION

The current setting of the Northern Cape study area has been driven primarily by Miocene to Pliocene 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 south-east, it falls entirely within the arid late summer rainfall region. Even so, the Northern Cape species pool shows multiple biogeographical origins along a south-west/north-east 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).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

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.

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

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).

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