

Dung beetle assemblage structure across the aridity and trophic resource gradient of the Botswana Kalahari: patterns and drivers at regional and local scales

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Abstract Understanding pattern and process at both regional and local scales is important for conservation planning although such knowledge of insects is frequently lacking. To assess patterns along a regional gradient of increasing aridity and diminishing food resources in the Botswana Kalahari, Scarabaeine dung beetles were sampled quantitatively using four dung types at three local sites in six regional areas. At regional scale, factor analysis of species abundance extracted a maximum of six factors, each dominated by a single area. Therefore, the statistical significance of regional spatial variation far outweighed that of dung type association. At local scale, six factor analyses of species abundance extracted from four to six factors. The importance of local dung type associations was relatively high but diminished with increasing local spatial heterogeneity. At regional scale, hierarchical analysis of oblique factors divided assemblages into unique local and shared regional components. Primary extended factors accounted for 40-50% of unique local faunal composition in five out of six areas. Two secondary extended factors showed either high shared proportional contribution to regional assemblage structure in the northeast with a steep decline to the southwest, or an opposite trend. Their point of intersection was consistent with a boundary zone between mesic northeast and arid southwest faunal components in the central Kalahari. Despite some inconsistencies in rank position between regression methods, rainfall, temperature, and mammal density / diversity were the strongest influences on regional patterns defined by secondary factors. Patterns are discussed according to conservation and changes in land usage around reserves.

Keywords: Aridity gradient · Assemblage structure · Botswana, Boundary · Dung beetle, Kalahari · Scarabaeinae

Introduction

Understanding pattern and process at both landscape and local scale is important for conservation planning (Tscharntke et al. 2012). However, data from which to evaluate macroecological patterns and their drivers is frequently limited or absent for insects (Diniz-Filho et al. 2010). Amongst the insects, which are a highly diverse taxon, dung beetles are considered an excellent focal indicator group for conservation studies since quantitative sampling requires relatively little effort and they show a degree of sensitivity to both spatial and trophic factors (Halffter and Favila 1993; Spector 1996). Therefore, to provide insights into pattern and process in dung beetle distribution along an 1170 km regional aridity and trophic resource gradient in the Botswana Kalahari, a detailed but coarse grained approach was adopted comprising local quantitative sampling at ~200 km intervals. Results may be considered to have been influenced on an evolutionary timescale by the geological and climatic history of the region, which is responsible for the current macroecological setting comprising an aridity and trophic resource gradient on deep sands, as well as by responses to current local functional ecological conditions.

The Kalahari deep sands (arenosols) cover much of central southern Africa (FAO/IIASA/ISRIC/ISSCAS/JRC 2012) and occupy the southern part of a sag basin that originated in late Cretaceous and early Cenozoic down-warping (Stokes et al. 1998; Haddon and McCarthy 2005). The widespread sand deposits overly earlier Kalahari Group sedimentary formations in the southern basin and result from Miocene and Pliocene uplift along its eastern edge that led to the exposure of sandstone and inward fluvial erosion. Wind

action, possibly during the Pleistocene, has resulted in much aeolian re-distribution of the sand into dune fields, particularly in the southwest. The uplift and deposition of sand coincided with the Pliocene development of the cold Benguela upwelling on the west coast and a possibly dryer climate in much of the southwest (Tyson 1986). This climatic system persists to the present day as the easterly wind currents that carry summer rainfall to the Botswana Kalahari (Tyson 1986) arrive increasingly later to the southwest resulting in an increasingly brief and seasonally later period of lower rainfall.

The distinctive regional edaphic and climatic character of the Kalahari might be predicted to have a strong influence on the composition of both the regional and local biota. This is partly supported by the roughly 80-90% coincidence between the Kalahari sands and three major ecoregions (Olson et al. 2001) comprising dry to mesic savanna in the northeast (AT0726: Zambezian *Baikiaea* Woodlands; AT0709: Kalahari *Acacia-Baikiaea* Woodlands) and arid savanna in the southwest (AT1309, Kalahari Xeric Savanna). The increasing aridity to the southwest is exacerbated by the absence or rarity of natural surface water (Moyo et al. 1993; Penry 1994) in central and southwestern regions, which limits the diversity of mammals (Ministry of Wildlife, Environment & Tourism 2004). It bars the occurrence of herbivores dependent on permanent water, such as buffalo and elephant (Campbell 1973; Chamaillé-Jammes et al. 2007) with their distinctive large dung types. It supports only water-efficient herbivores that drop their dung as pellets as well as their predators that produce small highly nitrogenous droppings. Southwestern Kalahari aridity on deep sands is also known to influence the biogeographical distribution of dung beetles in southern Africa since a group of psammophilous dung beetles has been demonstrated to be centred on this region (Davis 1997). Thus, the aridity gradient has strongly influenced species composition whereas the reduced diversity of dung types would also be expected to strongly influence dung beetle assemblages given that some Botswana species are known to be dung type specialists, particularly those attracted primarily to elephant dung (Tshikae et al. 2008).

The present study examines patterns of dung beetle assemblage structure in Kalahari game reserves across the northeast / southwest gradient of gradually increasing aridity and decreasing dung type diversity. The study was conducted within the borders of Botswana, which includes roughly 60% of the southern Kalahari deep sands. Study areas were selected according to the ecoregion classification of Olson et al. (2001), one in each of three northeastern ecoregions and three in the single southwestern ecoregion. The aims of the study were (1) to determine how dung beetle assemblage structure was influenced by regional and local factors across the gradient; (2) to define the transitional zone between northeast and southwest centres of dung beetle distribution and discuss the processes responsible; and (3) to discuss the implications for dung beetle conservation of both the results, recorded from game reserves, and changes in land usage in surrounding areas, particularly the erection of fences, which has strongly modified the former migratory system of large indigenous mammals into the Kalahari from northeast and southwest centres (Moleele and Mainah 2003; McGahey 2011).

Methods

Study region and gradsect

The gradsect study was conducted from northeast to southwest along an 1170 km gradient of increasing aridity and diminishing mammal diversity across the deep sands of the Botswana Kalahari. Six study areas were selected in three conserved regions proclaimed prior to 1966. Two areas were selected per reserve and three study sites per area (Fig. 1). Four different dung types were used as attractants to sample dung beetles (pig, elephant, cattle, sheep).

Physical and climatic factors

Altitude varies by only 150 m amongst study areas. Although it follows an irregular pattern along the gradsect, average annual temperature is uniformly higher in the northeast half of the gradsect compared to the southwest half (Fig. 2). By contrast, over the three summer months during which sampling of beetles was conducted (December to February), average daily temperatures increased to the southwest. However, like annual temperatures, average annual rainfall also shows a strong decline from the northeast (>600 mm per annum) to the arid southwest (<200 mm per annum) (Fig. 3). Most of the gradsect lay in the mid-summer rainfall region (Davis 1997 after Walter and Lieth 1964) but there is a slight seasonal shift from January peaks to a March peak in Transfrontier (Fig. 3), which lies at the edge of the southwestern arid late summer rainfall region (Tshikae 2011).

Landscapes, ecoregions and large mammal diversity

Two principal landscape types are represented across the aridity gradient (Wit and de Bekker 1990). Aeolian sand deposits dominate in the southwest and extreme northeast with the intervening northeastern area partly interrupted by the fossil lagoon systems of the Mababe (Savuti) and Mkgadigadi Depressions (North CKGR). As dung beetles are strongly influenced by soil texture (Nealis 1977; Davis 1996), soil grain-size profiles were measured from three cores taken at a depth of 20-30 cm from the ends and centre of each study site (3 samples x 3 sites x 6 areas = 54 samples).

According to the classification of Olson *et al.* (2001), the gradsect crosses three woodland ecoregions in the northeast of Botswana (Zambeziian *Baikiaea* Woodlands in Chobe, Zambeziian and Mopane Woodlands at Savuti, Kalahari *Acacia-Baikiaea* Woodlands in North CKGR) and a single arid ecoregion in the southwest (three study areas in Kalahari Xeric Savanna) with its northeast boundary lying in the central Kalahari (Olson *et al.* 2001; Fig. 4) bisecting the CKGR between North CKGR and Khutse. Although taxonomic structure of plant assemblages does not influence dung beetle assemblages, they are strongly influenced by vegetation structure, particularly classes comprising (1) unshaded grassland; (2) partially shaded open shrubland or woodland; or (3) strongly shaded thickets, woodland, or forest (Cambefort 1982; Davis 1996). Therefore, vegetation structure was measured at each study site. Surface cover was scored as present or absent depending on whether or not grass or herbs made contact with the boot tip at each of 100 paces. For woody vegetation cover, five sets of measurements were made at each site, one set for trees (classified as over 4.5 m in height) and one set for shrubs (classified as up to 4.5 m). For each of five selected trees or shrubs, the distance was measured from its centre to the centre of the four nearest neighbouring trees or shrubs in the cardinal directions of north, east, south, and west, with permitted deviation up to

$\pm 45^\circ$. In the case of a shrub, further measurements were made from the centre to its edge, then to the edge of the nearest neighbour and then to its centre. In the case of a tree, further measurements were made from the trunk to the edge of its canopy, then to the edge of the nearest neighbour's canopy and from the canopy edge to its trunk. These measurements were used to calculate percentage surface, shrub, and shade cover.

Species abundance composition of dung beetle assemblages is influenced by various factors relating to dung type. These include mammalian diet and resulting dung odour (Davis 1994; Dormont et al. 2010), dropping size (Peck and Howden 1984) plus amounts (Lumaret et al. 1992) and spatial frequency of droppings (Lobo et al. 2006). Therefore, variation in dung type availability across the gradsect was quantified using data on mammal diversity, mammal density, and dung type. Diversity and density of large mammals were determined from aerial survey census data for the three major conservation regions (Ministry of Wildlife, Environment & Tourism 2004). As predators are mostly nocturnal, their population sizes are not effectively estimated by daytime surveys. Therefore, cited information for the northern and southern regions has been extracted from other published gross estimates for predators (Botswana Central Statistics Organization 2005). Large mammal density has also been expressed in terms of biomass using average body mass data for mammal species published by Skinner and Chimimba (2005). Dung type variability was categorized by large mammal digestion type, diet, dropping size and texture, using the simple classification of Davis and Scholtz (2001).

Trapping sites and trapping method

Twenty 5 L pitfall traps (top diameter = 22 cm, depth = 16 cm) were placed in a 2 x 10 grid at each of the 18 study sites (Supplementary Fig. 1) where they were sunk into the sand up to their rims. Each trap was separated by 50 m, following the recommendations of Larsen and Forsyth (2005). Dung beetles were attracted using five easily-obtained bait types representing different classes of food type. They were placed separately on traps in the order of pig dung (omnivore), cattle dung (ruminant herbivore - pads), elephant dung (monogastric herbivore - fibrous droppings), carrion (results not reported here), and sheep dung (ruminant herbivore - pellets), repeated four times. A standard size was used for all dung baits irrespective of natural dropping size. These comprised circa 250 mls wrapped in thin cloth to exclude dung beetles but permit release of odours. Baits were frozen and thawed before use except for elephant dung, which was collected fresh just before each sampling exercise. Baits were supported at ground level over the centre of each trap using two strong wires.

Because of the slight differences in timing of seasonal rainfall peaks across the gradsect, sampling of dung beetles was conducted at an earlier date in the northeast (December 2005 - Chobe, Savuti) and centre (January 2006 - North CKGR, Khutse) than in the southwest (February 2006 - Mabuasehube, Transfrontier). Sampling was conducted over 48 h periods. Pitfall traps were baited or re-baited in the early morning and late afternoon to present fresh dung to both diurnal and nocturnal dung beetle species. Beetles were immobilized using water and a little detergent in the base of each trap. Samples were removed and stored in alcohol after each 24 h period.

Analysis of regional patterns

The data set is considered to be comprehensive as species accumulation was near asymptote in all 24 study area x dung type combinations tested by sample-based rarefaction (Tshikae 2011). Regional patterns of spatial and trophic distribution were defined using Factor Analysis with principal components used to extract factors. The 132 x 72 raw data matrix comprised mean abundance / trap / day for 132 species attracted to each of four dung types at three study sites in each of six study areas ($4 \times 3 \times 6 = 72$). The matrix was 4th root transformed and converted to a 72 x 72 correlation matrix before ordination analysis. Six factors were the maximum that could be extracted.

As oblique factors are often difficult to interpret, we conducted a Hierarchical Analysis of Oblique Factors (see Wherry 1984). Varimax-normalized rotation of factors through six clusters of data points was first used to maximize between-cluster variance. Rotated, oblique factor loadings were then subjected to a second Factor Analysis to generate extended orthogonal factors. Correlations (r^2) between extended orthogonal and oblique factor loadings were used to determine the proportion of unique character contributed by primary (P) extended factors within each cluster, and the proportion in common with other clusters, due to shared secondary (S) factors.

Analysis of local patterns

Patterns of local spatial and trophic distribution were defined using Factor Analyses of species abundance data for each of the six study areas. The raw data matrices comprised mean abundance / trap / day for the species attracted to each of four dung types at the three study sites in each study area (Chobe: 67 species x 48 traps, Savuti: 68 x 48, North CKGR: 44 x 48, Khutse: 59 x 48, Mabuasehube: 45 x 48, Transfrontier: 38 x 48). These matrices were 4th root transformed and converted to 48 x 48 correlation matrices before ordination following the same procedure as for the regional analysis. Four factors were the maximum that could be extracted from data for four areas with five and six factors the maxima that could be extracted from the other two.

Analysis of spatial and trophic influences

GLM ANOVAs were used to determine the influence of spatial variables and dung type on rotated oblique factor loadings for both regional and local scale analyses. In the regional scale analysis, four standard dung types were nested within six regional study areas on the assumption that regional faunal exchange was unlikely whereas there was a possibility of local faunal exchange. Local study sites were not included as a factor in this analysis since their ecological character could not be standardized across the region. Separate analyses for each study area were conducted to determine the influence of local spatial variables versus dung type association using a factorial GLM ANOVA.

Multiple and linear regressions were used to determine correlations between five environmental factors and loadings for secondary extended factors from the regional scale analysis. These factors described close to straight line distributions and represented shared regional trends after removal of unique local effects. Environmental factors 1-3 comprised 4th root transformed data for (1) average annual rainfall, (2) average temperature during the sampling period between December to January, and (3) percentage of sand at each of 18 study sites (six study areas x three study sites). Environmental factors 4-5 comprised indices derived from NMDS ordination in which a single

dimension was generated for (4) woody vegetation density at each of the 18 sites derived from a raw data matrix for densities of trees (five measurements) and shrubs (five measurements), and (5) mammal species density / diversity derived from a raw data matrix for densities of 25 mammal species in Chobe National Park, Central Kalahari Game Reserve, and Kgalagadi Transfrontier Park (Supplementary Table 1). Owing to problems associated with the use of these classic parametric regression techniques (Hawkins 2012), the results were compared with those from regression tree analysis (Breiman et al. 1998), which does not assume any underlying distribution pattern in the data. Although this analysis was used to rank the overall effects of environmental factors on dependent variables (ordination factors), neither this method nor any other is able to distinguish between causality and mere co-linearity.

Results

Soil texture, vegetation cover, and mammal distribution patterns

Across the gradsect, grain size analysis showed there were only minor differences amongst soil profiles, all of which, on average, comprised over 94% coarse sand (sample range = 91-100%) and only very small proportions of silt and clay (Table 1). After removal of data for non-soil inclusions (% other) and re-scaling of values for the three grain sizes to 100%, GLM one-way ANOVA showed that there were no significant differences between percentages of sand at study areas ($F_{(5, 48)} = 2.3, P=0.057$). These adjusted averages for sand were: Chobe 97.1%, Savuti 98.0%, North CKGR 97.4%, Khutse 99.6%, Mabuasehube 99.1%, Transfrontier 98.2%.

Along the gradsect, tree canopy shade cover was a dominant characteristic only in the Zambebian *Baikiaea* Woodlands of the extreme northeast in Chobe (Table 2). Elsewhere, dominant woody vegetation comprised mostly open shrubland including in Zambebian and Mopane Woodlands on the lacustrine sands around Savuti and in Kalahari *Acacia-Baikiaea* Woodlands of North CKGR where sparse tree cover occurred only at site 3. The Kalahari Xeric Savanna was dominated by open grassland and scattered shrubs although large trees occurred at Site 3 in Transfrontier, where they were associated with a dry river bed. In general, mean density of woody vegetation declined across the aridity gradient. GLM one-way ANOVAs showed that decline in the density of shrubland cover was significant ($F_{(5, 84)} = 23.728, P<0.001$) whereas significant differences in grass cover ($F_{(5, 12)} = 4.755, P<0.05$) were limited to the most arid study area in Transfrontier.

Of 25 large, indigenous, terrestrial mammal species, 21 were recorded in Chobe National Park, 16 in CKGR, and 13 in Kgalagadi Transfrontier Park (Supplementary Table 1). In addition to the decline in diversity and biomass of large indigenous mammal species from northeast to southwest, the diversity of dung types also declines (Table 3). Two dung types are not represented in the indigenous mammal fauna of the central and southwest regions beyond Lake Ngami (20° 30'S 22° 40'E) (Kalahari *Acacia-Baikiaea* Woodlands and Kalahari Xeric Savanna: large fine-fibred pads of large ruminant herbivores - African buffalo; large coarse-fibred droppings of large monogastric herbivores - elephant, Burchell's zebra) (Table 3). Only carnivores and pellet-dropping indigenous mammals are represented in reserves of this central and southwestern region. However, owing to the presence of nearby farms, minor incursions of pad-dropping domestic ruminants (cattle) were recorded at the margins of central and southwest reserves in 2004 (southern CKGR - 0.06 individuals / km²; Transfrontier - 0.03 individuals / km²) (Supplementary Table 1).

Dung beetle distribution patterns

Factor analysis of regional dung beetle data accounted for over 80% of the variance. Clustering of data points for species assemblages showed a strong separation between each of the six study areas irrespective of the dung type to which they were attracted (Fig. 5, Table 4). GLM nested ANOVA indicated that regional spatial factors across the aridity gradient were by far the strongest significant influence on factor loadings (Table 4). Even so, except in the most arid study area at Transfrontier, there were significant local differences between factor loadings for dung type. The higher F values for study areas in Chobe (northeast mesic savanna) and Transfrontier (southwest arid savanna) reflect the great differences in dung beetle species composition and relative abundances at the extremes of the gradsect across which there was a decline from 67 species in the northeast to 38 in the southwest (Table 4). The dip in F values in the Central Kalahari reflects the lower significance of differences between assemblages in the centre of the gradsect.

In most cases, there was a similar proportional amount of unique structure in species assemblages in each study area (P factors: 41-50%) except at Mabuasehube (21%) (Table 5), which was the intermediate study area within the Kalahari Xeric Savanna ecoregion (Fig. 4). However, two shared (S) factors showed different trends in proportional composition between study areas. Factor S1 showed greatest contribution to species assemblages in the arid southwest and declined to the mesic northeast whereas factor S2 showed an opposite trend. Shared southwestern faunal character was minimal in Chobe National Park (Chobe, Savuti - 0% to 1%) whereas shared northeastern faunal character was minimal in the Transfrontier Park (Mabuasehube, Transfrontier - 0% to 2%) (Table 5). There was somewhat more equitable representation of shared southwest and northeast faunal character in the Central Kalahari Game Reserve (21% and 36% in North CKGR, 48% and 12% in Khutse). Lines fitted to data points for these shared factors (Fig. 6) intersected in the Central Kalahari Game Reserve between Khutse and North CKGR close to the boundary between the Kalahari Xeric Savanna and Kalahari *Acacia-Baikiaea* woodland ecoregions (Fig. 4).

Loadings for secondary extended factors (S1, S2) were significantly influenced by environmental factors (Table 6) and accounted for a great deal of the variation between study areas (Table 6A). Both linear regression (Table 6B) and regression tree analysis (Fig. 7) indicated some inconsistency in the rank order of correlation with different environmental variables. However, in all analyses, rainfall, sampling temperature, and mammal density / diversity were variously the strongest significant correlates with smaller contributions from woody vegetation cover and soil texture. For secondary factors showing higher loadings in the southwest, correlations with environmental factors were negative for rainfall, mammal density / diversity and woody vegetation cover and positive for temperature and soil texture (Table 6B). For the factor showing higher loadings in the northeast, an opposite trend was shown.

Classification of assemblage structure within each of the six study areas (Supplementary Table 2) showed that both spatial variation and dung type associations were important local influences compared to the extreme dominance of spatial factors at regional scale (Table 7). Overall, spatial variation had a greater local influence within three areas (Chobe, North CKGR, Transfrontier) whereas dung type was a greater local influence at the other three

(Savuti, Khutse, Mabuasehube). Although there were some significant interactions between space and dung type, these had a much more limited influence compared to each separate variable. At Chobe, there was strong factorization according to dung type at the two less shaded sites (Table 8 - sites 2, 3) with spatial differences dominating for all dung types at the most shaded site 1 (Supplementary Table 2). Limited spatial heterogeneity on the fossil lake bed at Savuti was reflected by the dominance of factorization according to dung type (Table 7) although there was limited spatial variability imposed by site 3 (Supplementary Table 2 - Factor 3) with its significantly denser shrub cover (Table 8). There was limited factorization according to dung type on isolated dunes at North CKGR (Table 7, Supplementary Table 2) with most variation imposed by spatial differences at site 3 with its significantly greater woody vegetation cover (Table 8). At Khutse, there was clear factorization according to dung type (Supplementary Table 2) but spatial variation was only slightly less influential (Table 7) due to differences between sites closest (site 3) and most distant (site 1) from the reserve boundary that mostly affected results for cattle dung. Woody vegetation cover showed no significant differences between study sites (Table 8). At Mabuasehube, factorization was entirely dominated by dung type (Table 7, Supplementary Table 2) despite significantly greater woody vegetation cover at site 3 (Table 8). Although woody vegetation cover did not differ significantly in the dune field at Transfrontier (Table 8), there was extensive heterogeneity both spatially and trophically (Table 7, Supplementary Table 2). Factorization according to dung type dominated at site 2 with spatial differences dominating at site 3 with results for site 1 intermediate.

Discussion

Kalahari dung beetle diversity

The southwest Kalahari has previously been identified as a centre of dung beetle endemism using presence or absence data (Davis 1997). The present analyses of quantitative data showed that regional changes in dung beetle assemblage structure were especially strongly correlated or co-linear with increasing aridity, increasing temperatures, and decreasing mammal diversity / density, from northeast to southwest across the southern Kalahari. At both regional and local scale, patterns of dung type association were also important organizers of assemblage structure although their effects were diminished by increasing local spatial heterogeneity caused by differences in density of woody vegetation cover and other unidentified or unmeasured factors that may include local density of dung.

Division of Kalahari assemblage structure into shared regional and unique local variation provided insights into the relative conservation value of each of the three reserves of Chobe National Park, Central Kalahari Game Reserve and Kgalagadi Transfrontier Park. There was a high degree of unique local assemblage structure at each of six study areas within the reserves except at Mabuasehube. Furthermore, shared regional variation comprised two clear faunal components with opposing distributional trends of declining proportional representation of the northeast component to the southwest and the opposite for the southwest component. The minimal values for the northeast component in the southwest reflect replacement of northeast mesic savanna species by southwest arid savanna species and vice versa (Tshikae et al. unpublished). These trends account for the extreme differences in faunal structure at the gradsect endpoints.

Lines that connect values for the shared regional components intersect in the Central Kalahari Game Reserve between North CKGR and Khutse Game Reserve close to the defined edges of the Kalahari Xeric Savanna and Kalahari *Acacia-Baikiaea* Woodland ecoregions (Olson et al. 2001; National Geographic 2001). This intersection provides strong support for what would be defined by Strayer et al. (2003) as a tangible contemporary ecological boundary that is characterized by a zone of overlapping northeast and southwest influences in the central Kalahari. Northeast / southwest polarization in assemblage structure is supported by a biogeographical analysis of the fauna recorded across the gradsect (Tshikae 2011). The southwest was dominated by species forming a single biogeographical unit showing limited distributional overlap with the different species of several other biogeographical units that dominated in the northeast and showed appreciable distributional overlap with one another.

Relative importance of different environmental factors

By a consideration of regional evolutionary history and dung beetle functional ecology, we attempt to elucidate some of the processes responsible for the patterns, which may be tested by further work to assist conservation decisions. It should be noted that irrespective of significant correlations shown between factor loadings and environmental factors, their co-linearity is not necessarily indicative that a particular environmental factor was an ecologically important determinant of dung beetle assemblage structure.

Soil texture has the capacity to strongly influence dung beetle assemblage structure (Nealis 1977; Davis 1996) owing to differences in particle size profiles that influence drainage rate, moisture-holding capacity, the duration of moisture retention, and relative hardness, which facilitates or hinders the excavation of tunnels (Hanski and Cambefort 1991) and the survival of immatures (Fincher 1973). In the present study, there was only minor variation between soils as all sites were dominated by sand. However, soil texture was identified as a significant regional influence. This may reflect differences in species representation between aeolian and lacustrine sands that appeared to be independent of other physical factors across the gradsect. For instance, the large roller, *Pachylomera femoralis* (Kirby) and four other species were well represented on aeolian sands in the moist northeast woodlands of Chobe and the dryer southwest shrublands of Khutse but very poorly represented on intervening lacustrine sands in the shrublands of Savuti and on parabolic dunes (40% of area) at the edge of the lacustrine system of the Mkgadigadi Depression (Supplementary Table 3). This suggests that some unmeasured characteristic of these areas of aeolian and lacustrine sands may influence the occurrence of some dung beetle species. There was also lower abundance and the essentially unique occurrence of a number of species on lacustrine sands (Savuti, North CKGR) (Supplementary Table 3). However, other than for *Copris elphenor* Klug, which is known to be equally abundant in open woodland and grassland (Davis 1996), there is insufficient evidence to determine if the occurrences of these species are linked exclusively to edaphic factors or also to vegetation cover and climatic factors.

Vegetation cover strongly influences dung beetle assemblage structure (Cambefort, 1982; Davis, 1996). The differences may variously be responses to the different microclimatic conditions under shade (lower light intensity and temperatures, higher humidity than in grassland - Davis et al. 2003) or to increased rate of soil moisture loss and higher surface temperatures in sparsely grassed open habitats (Jankielsohn et al. 2001). There

were significant trends in vegetation cover across the present gradsect and significant correlations were indicated between woody vegetation cover and factor loadings representing dung beetle assemblage structure. Chobe was situated in the Zambezian *Baikiaea* Woodland ecoregion and was the only study area characterized by a tree canopy. This undoubtedly influenced assemblage structure at the northeast extreme of the gradsect. Several widespread species known to show a bias to shaded habitats (Davis 1996) were much more abundant at the most densely shaded study site in Chobe than in the less shaded sites (e.g. *Anachalcos convexus* Boheman, *Onthophagus vinctus* Erichson). They were also rare in the shrublands of Savuti and points further to the southwest. It is also likely that some geographically widespread species recorded in the northeast and southwest shrublands, and known to be associated with open habitats (Davis 1996), were excluded from Chobe owing to the tree shade cover (e.g. *Allogymnopleurus thalassinus* Klug, *Gymnopleurus aenescens* Wiedemann). However, across the gradsect, significant differences in density of woody vegetation and grassland cover were primarily at the northeast and southwest extremes, respectively, whereas the major boundary region was in the central Kalahari.

The complementary patterns of decrease in rainfall and increase in temperature to the southwest would be important mediators of dung beetle activity as dung beetle species richness and abundance increase after substantial rainfall (Davis 1995; 2002), when there are more equitable temperatures for activity and softer, more malleable soil for tunneling. As coincidence of rainfall events with suitable temperatures are the drivers of seasonality in dung beetle activity (Cambefort 1991; Davis 2002) sampling of dung beetles was offset over mid to late summer to accommodate the seasonal shift in rainfall peaks from northeast (January) to southwest (February / March) across the gradsect. However, decreasing frequency of rainfall events and increasingly drier climate across the aridity gradient results in fewer occasions when conditions are suitable for activity. This may or may not be directly responsible for the lower species richness of assemblages in the more arid extremes of warm temperate climate in southern Africa (Davis 1997) that includes the southwest Kalahari (Tshikae 2011). This is not merely a filtering out of northeastern-centred mesic savanna species with strategies less suited to arid conditions but a replacement by psammophilous arid-adapted, southwest-centred species that are filtered out to the northeast (Tshikae et al. unpublished). Only a few species are common to both the northeast and southwest assemblages resulting in low levels of similarity between assemblages at the extremes (similarity between Chobe and Transfrontier = 15.5% species composition, 10.2% species abundance structure). Although the rainfall gradient might maintain the status quo, it may not be responsible in itself for the boundary region unless the assemblages were composed from rearrangement of ranges of pre-existing species in the recent historical past, known to have occurred in other taxa at the end of the African Pleistocene (Livingstone 1975), rather than from speciation *in situ*, which is an historical process operating over an evolutionary timescale. As the southwest Kalahari is a centre of endemism for dung beetles (Davis 1997; Tshikae 2011), at least some *in situ* speciation seems a likely scenario.

As the natural mammal fauna of the central and southwestern Kalahari is composed of pellet-dropping herbivores and predators voiding small nitrogenous rich droppings, the correlations between factor loadings and mammal diversity indices probably reflect real influences on the dung beetle fauna, particularly as it is known that some species show strong biases towards particular dung types (Davis 1994; Tshikae et al. 2008) and some are centred on game reserves containing elephants (Davis 1997) whose dung types are absent from the southwest

Kalahari. The importance of regional differences in mammal and dung type diversity is strongly suggested by the endemic nature of the southwestern fauna (Tshikae 2011) and its different manner of partitioning the same dung resources either side of the central Kalahari boundary zone (Tshikae 2011, Tshikae et al. In press). Locally, low amounts and low density of droppings reduce species richness and abundance of dung beetles (Lobo et al. 2006) compared to localities with greater density and amounts of dung. This may account for the particularly low values for the assemblage recorded in North CKGR, which was an interruption in the otherwise gradual northeast / southwest decline in regional dung beetle species diversity (Tshikae et al. unpublished).

During recent history, the gradient of decreasing mammal density and diversity was probably maintained by lower rainfall and, especially, by the absence or rarity of surface water to the centre and southwest, except after heavy rainfall (Moyo et al. 1993; Penry 1994). This resulted in a decrease in diversity and size of dung types owing to the exclusion of large monogastric (elephant, rhinoceros, zebra - large coarse-fibred droppings) and large ruminant herbivores (buffalo - large moist pads) that need to drink frequently from permanent sources of water. As herbivore pellets dominate in the central and southwestern region (including those of four species not recorded to the northeast - Supplementary Table 1), the present results probably reflect dung beetle responses to these patterns on both evolutionary (origins of regional species pool) and current functional ecological timescales (local responses to type and density of dung), including the response to elephant and cattle dung baits in the southwest where they represent an experimental presentation of dung types that do not occur naturally in the region. However, although the results were obtained from conserved areas, one must also consider the possible influence of factors resulting from recent commercial development across the Kalahari.

Human impact in recent decades

Until the recent past, various mammal species were able to migrate within the Botswana Kalahari from both southwest and northeast centres (Campbell 1973; Moleele and Mainah 2003). It is hypothesized that these movements permitted the exploitation of new growth vegetation in areas where rain had fallen during the summer rainy season (Verlinden and Masogo 1997). In order to prevent the spread of livestock diseases and protect the beef export industry to the European Union (Mbaiwa and Mbaiwa 2006), routes from the northeast began to be interrupted by veterinary fences from 1954 continuing until 1996 (McGahey 2011) (see Fig. 1 for the most southwestern of 17 fences). Thus, routes towards and from the central Kalahari were cut, leading to a precipitous decline in indigenous mammal densities in the 1960s (Main 1987; Albertson 1998). Fenced ranching areas to the south of the Dibete and Kuke fences were scattered throughout the Kalahari without creating a complete barrier. However, between 1976 and 1979, all southern areas outside of reserves were gazetted for communal grazing, fenced ranching, or wildlife management (Wallgren et al. 2009). Recent surveys in the Kgalagadi North district that lies across migratory routes between the Transfrontier Park and the CKGR indicate steep declines in most large indigenous mammals due to expansion of the livestock sector, increasing hunting pressure, drought, declining surface water, and the presence of cordon fences (Moleele and Mainah 2003). It is not possible to determine if these developments influenced the present results. The reasons for particularly low dung beetle abundance in North CKGR could be related to declines in indigenous mammal density due to veterinary cordon fences. Furthermore,

analysis of local patterns at Khutse showed spatial differences in assemblage structure on cattle dung for sites closer or further from the edge of the reserve. As these patterns were not repeated for other dung types, it is possible that results were influenced by limited incursions into southwestern reserves by cattle and other domestic livestock (Supplementary Table 1) that have been supported by borehole water on nearby farms since 1975 according to official estimates (Perkins 1996). Thus, further work at more localized scales is required to examine the effects of changing land usage, particularly gradsects from communal rangeland into the centre of each reserve that measure dung beetle assemblages and both the diversity and density of the indigenous or domestic mammal faunas that provide their food resource.

Synthesis

Across conserved regions of the Botswana Kalahari, it is likely that the strongest influences on changing dung beetle assemblage structure are the co-varying changes in climate and mammal diversity. Strongest correlations were shown jointly by the gradient of declining frequency and amount of rain to the southwest and the parallel gradient of increase in daily temperatures during the summer when dung beetles are actively colonizing dung. Thus, species centred in the southwest are exposed to hotter dryer conditions and less frequent rainfall events than those in the northeast. The rarity of surface water in the central and southwestern regions also results in a natural decrease in mammal species diversity, mammal density, and dung type diversity. Under natural conditions, only herbivore pellets and carnivore droppings are available compared to the additional availability of large moist pads and large fibrous droppings of large ruminant and monogastric herbivores in the northeast. This decline in frequency of suitable conditions for activity and reduction in trophic resources to the southwest is presumably responsible for the decline in dung beetle species richness and diversity, increasing endemism, and differing patterns of trophic resource partitioning (Tshikae 2011; Tshikae et al. In press) between northeast and southwest assemblages that are largely composed of different species. These patterns constitute a strong case for the continuing conservation of northeast and southwest extremes of the Kalahari together with the central overlap zone.

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Table 1 Landscape type and soil texture analysis in six study areas across the Botswana Kalahari

Study area	Soil texture (grain size range)				Landscape classification (Wit and de Bekker 1990)
	% sand	% silt	% clay	% other	
Chobe	94.5 ±2.0	1.2 ±1.7	1.5 ±1.7	2.7 ±1.2	Aeolian sand (Sa21) almost flat to gently undulating plain
Savuti	96.2 ±2.6	0.5 ±0.4	1.5 ±1.5	1.9 ±1.6	Lacustrine sand (L15) almost flat fossil lagoon
North CKGR*	95.8 ±2.8	0.8 ±0.7	1.7 ±1.5	1.7 ±1.1	Lacustrine sand (L15) almost flat fossil lagoon
Khutse	99.2 ±0.7	0.0	0.4 ±0.5	0.3 ±0.4	Aeolian sand (Sa19) undulating parabolic dunes, fossil rivers
Mabuasehube	98.6 ±1.4	0.5 ±0.6	0.4 ±1.0	0.3 ±1.2	Aeolian sand (Sa11) almost flat plain, calcrete depressions
Transfrontier	96.5 ±2.4	1.0 ±0.1	1.7 ±2.0	1.7 ±1.3	Aeolian sand (Sa15) flat / almost flat fossil valley system
					Aeolian sand (Sa4) almost flat plain, few pans
					Aeolian sand (Sa11) almost flat plain, calcrete depressions
					Aeolian sand (Sa1) undulating to rolling longitudinal dunes

*Although the North CKGR study area straddled the edges of aeolian and lacustrine systems, all study sites were on dunes.

Table 2 Vegetation density across the Botswana Kalahari aridity gradient

Locality	Dominant vegetation	Mean % cover ±SD		
		Tree canopy	Shrubs [^]	Grass ^{^^}
Chobe	<i>Baikiaea plurijuga</i> woodland	60.4 ±16.8	38.4 ±11.7 ^b	38.0 ±5.3 ^{ab}
Savuti	<i>Colophospermum mopane</i> shrubland		62.5 ±18.8 ^a	33.9 ±11.1 ^{ab}
North CKGR	Grassland, scattered trees and shrubs	12.7*	37.4 ±12.4 ^b	54.2 ±2.1 ^a
Khutse	Grassland, scattered shrubs		34.9 ±12.6 ^b	59.3 ±24.7 ^a
Mabuasehube	Grassland, scattered shrubs		26.0 ±11.3 ^{bc}	58.1 ±5.3 ^a
Transfrontier	Grassland, scattered trees and shrubs	5.9*	13.8 ±7.4 ^c	18.9 ±13.9 ^b

*For spot tree cover density at North CKGR: Site 3 and Transfrontier: Site 3, see Table 8.

[^] ^{^^} Shrubland or grass cover values followed by a different letter differed significantly ($P < 0.05$ Tukey's HSD).

Table 3 Density of indigenous mammals in three conservation regions of Botswana during 2004 (see Supplementary Table 1)

Diet / digestion type [^] (number of species)	Density of mammals: n / km ² (biomass: kg / km ²)		
	Chobe N.P. 10 589 km ²	CKGR 55 300 km ²	Kgalagadi Transfrontier 28 000 km ²
Monogastric herbivore (2+1)*	3.17 (5260.8)	0.00	0.00
Ruminant herbivore (pads) (1)	1.00 (450.5)	0.00	0.00
Ruminant herbivore (pellets) (13+1)**	0.39 (166.6)	1.01 (288.6)	1.87 (452.9)
Carnivore / omnivore (7)	0.05 (3.4)	0.31 (16.0)***	0.06 (3.0)

*Warthog included, **Giraffe included, ***Dominated by insectivores

[^]Large monogastric, non ruminant herbivores > large coarse-fibred droppings; large ruminant herbivores > moist, fine-fibred pads; large and small herbivores (mostly ruminants) > dry pellets; mammals with a meat (carnivore) or mixed meat and vegetable diet (omnivore) > small, strongly-odoured droppings (Davis and Scholtz 2001).

Table 4 Mean statistical distances between clusters of data points defined from ordination of abundance data for 132 dung beetle species (see Fig. 5); results for GLM ANOVA on four standard dung types nested within each of six study areas; and number of dung-associated species in each study area

Study areas - NE to SW (number of species)	Mean oblique rotated factor loadings for clusters of data points \pm SD [^]					
	Factor 2	Factor 5	Factor 4	Factor 3	Factor 6	Factor 1
Chobe (67)	0.827 \pm 0.039^a	0.278 \pm 0.090 ^b	0.154 \pm 0.078 ^{cd}	0.148 \pm 0.119 ^c	0.024 \pm 0.071 ^d	-0.002 \pm 0.033 ^d
Savuti (68)	0.270 \pm 0.045 ^b	0.797 \pm 0.054^a	0.212 \pm 0.092 ^b	0.061 \pm 0.059 ^d	0.044 \pm 0.094 ^d	-0.002 \pm 0.027 ^d
North CKGR (44)	0.163 \pm 0.049 ^c	0.247 \pm 0.110 ^b	0.769 \pm 0.041^a	0.199 \pm 0.072 ^c	0.161 \pm 0.074 ^c	0.139 \pm 0.043 ^c
Khutse (59)	0.155 \pm 0.073 ^c	0.071 \pm 0.050 ^c	0.181 \pm 0.042 ^{bc}	0.810 \pm 0.031^a	0.267 \pm 0.091 ^b	0.187 \pm 0.058 ^c
Mabuasehube (45)	0.029 \pm 0.055 ^d	0.055 \pm 0.049 ^{cd}	0.207 \pm 0.047 ^{bc}	0.360 \pm 0.041 ^b	0.740 \pm 0.041^a	0.389 \pm 0.055 ^b
Transfrontier (38)	-0.003 \pm 0.023 ^d	-0.004 \pm 0.038 ^d	0.112 \pm 0.065 ^d	0.156 \pm 0.057 ^c	0.221 \pm 0.083 ^{bc}	0.866 \pm 0.043^a
ANOVA results						
Area $F_{(5, 48)}$	710.381***	377.212***	334.376***	310.692***	279.578***	775.380***
Dung (Area) $F_{(18, 48)}$	3.128***	3.831***	4.231***	3.406***	4.487***	1.686

*** $P < 0.001$. [^]Values followed by a different letter in each column differed significantly (Tukey's HSD). Along each factor, maximal loadings were consistent for single study areas (in bold) and showed significant separation ($P < 0.05$).

Table 5 Correlation coefficients (Pearson's r) and coefficients of determination (r^2) for regression of oblique factor loadings on extended orthogonal factor loadings from hierarchical analysis of oblique factors (see methods)

Oblique factors>>> Study areas>>> Extended factors	Factor 2 Chobe [^] r (r^2)	Factor 5 Savuti [^] r (r^2)	Factor 4 North CKGR [^] r (r^2)	Factor 3 Khutse [^] r (r^2)	Factor 6 Mabua. [^] r (r^2)	Factor 1 Transf. [^] r (r^2)	Influence
Secondary Factor S1	0.09 (0.01)	0.07 (0.00)	0.46 (0.21)	0.70 (0.48)	0.88 (0.77)	0.71 (0.50)	SW regional
Secondary Factor S2	0.72 (0.52)	0.77 (0.58)	0.60 (0.36)	0.34 (0.12)	0.16 (0.02)	-0.01 (0.00)	NE regional
Primary factors P1-6	P2 ^{^^} 0.68 (0.47)	P5 ^{^^} 0.64 (0.41)	P4 ^{^^} 0.66 (0.43)	P3 ^{^^} 0.63 (0.40)	P6 ^{^^} 0.46 (0.21)	P1 ^{^^} 0.71 (0.50)	Local unique

[^]Reserves ranked from NE to SW. ^{^^}n.b. All other values for regression of oblique factor loadings on primary extended orthogonal factor loadings were zero.

Table 6 Statistics from multiple and linear regression of environmental factors on secondary (shared) extended factor loadings for dung beetle assemblages (Fig. 6 - S1, S2, with, respectively, southwest or northeast regional bias)

A. Multiple regression

Relationships between environmental and ordination factors (Wilk's tests)

Ordination factors	F	adjusted r^2
Factor S1 (SW) - $F_{(5, 66)}$	58.676***	0.802
Factor S2 (NE) - $F_{(5, 66)}$	220.462***	0.939

B. Linear regression

Environmental influences on each ordination factor

Environmental factors	Ordination factors t and r^2 values	
	S1 (SW) $t_{(70)}$	S2 (NE) $t_{(70)}$
Annual rainfall	-12.365***	19.976***
Mammal density/diversity	-10.178***	6.082***
Summer temperature	8.503***	-15.390***
Woody vegetation density	-5.376***	4.380***
Soil texture (% sand)	3.897***	-2.390**

Environmental factors	S1 (SW) r^2	S2 (NE) r^2
Annual rainfall	0.68	0.85
Mammal density/diversity	0.59	0.34
Summer temperature	0.50	0.77
Woody vegetation density	0.28	0.20
Soil texture (% sand)	0.16	0.10

** $P < 0.01$, *** $P < 0.001$

Table 7 Results for GLM factorial ANOVA (Wilk's tests) comparing distances between dung beetle assemblages at three study sites on four dung types in six study areas across the Botswana aridity and trophic resource gradient (distance loadings derived from separate regional (one) and local (six) factor analyses)

Study area	F^{\wedge}		
	Space	Dung	Space*Dung
Regional Areas			
All study areas	861.131***	9.122***	2.004***
Local Sites			
Chobe	40.246***	19.258***	3.974***
Savuti	17.174***	39.257***	1.318
N CKGR	39.873***	15.032***	2.318***
Khutse	14.036***	21.249***	0.316
Mabuasehube	10.070***	73.610***	4.380***
Transfrontier	44.588***	32.603***	2.708***

$^{\wedge}F$ numbers derived from Wilk's tests on loadings for six factors (All study areas F_{30} , F_{18} , F_{90} ; Transfrontier F_{12} , F_{18} , F_{36}), five factors (North CKGR, F_{10} , F_{15} , F_{30}) or four factors (all other study areas, F_8 , F_{12} , F_{24}) (see Supplementary Table 2 for classification of local patterns). *** $P < 0.001$.

Table 8 Woody vegetation cover at three study sites in each of six study areas across the Botswana aridity and trophic resource gradient with results for GLM one-way ANOVA

	Site1	Site 2	Site 3	$F_{2,12}$
Trees				
Chobe	68.7 ± 20.9	49.6 ± 10.7	62.8 ± 14.1	1.916
N CKGR	-	-	38.2 ± 10.7	-
Transf.	-	-	17.8 ± 4.4	-
Shrubs				
Chobe	35.9 ± 3.9	33.3 ± 19.0	44.1 ± 10.9	0.970
Savuti	58.7 ± 18.2 ^b	47.8 ± 7.0 ^b	80.9 ± 12.3 ^a	8.014**
N CKGR	27.0 ± 4.1 ^b	35.9 ± 10.6 ^b	48.7 ± 10.4 ^a	7.514**
Khutse	28.9 ± 10.9	41.9 ± 15.3	33.8 ± 9.7	1.454
Mabua.	21.4 ± 10.7 ^b	19.8 ± 5.6 ^b	36.8 ± 8.8 ^a	5.911*
Transf.	10.3 ± 4.1	15.1 ± 11.0	14.3 ± 5.2	0.583

* $P < 0.05$, ** $P < 0.01$. Values in each line followed by a different letter differed significantly ($P < 0.05$, Tukey's HSD).

Figure legends

Fig. 1 Map showing the location of study sites and study areas within conserved regions across the Botswana Kalahari with the location of two veterinary cordon fences (McGahey 2011) that have bisected Botswana since 1958

Fig. 2 Average annual and average monthly rainfall in six study areas across the aridity gradient of the Botswana Kalahari

Fig. 3 Average daily temperatures (max. + min. / 2) in six study areas across the Botswana Kalahari

Fig. 4 Map showing the ecoregions of Botswana after Olson et al. (2001) and National Geographic (2001) with the point of intersection (North CKGR to Khutse) between dominance of southwestern versus northeastern faunal components in dung beetle assemblages (see Fig. 6)

Fig. 5 Ordination plot showing statistical distances between dung beetle assemblage structure at three study sites within six study areas

Fig. 6 Points of intersection in the central Kalahari between regression lines joining shared southwest versus shared northeast components of dung-associated beetle assemblages, fitted using the distance-weighted least squares method

Fig. 7 Overall relative importance of correlations between environmental factors and secondary extended factors for dung beetle distribution determined from regression tree models

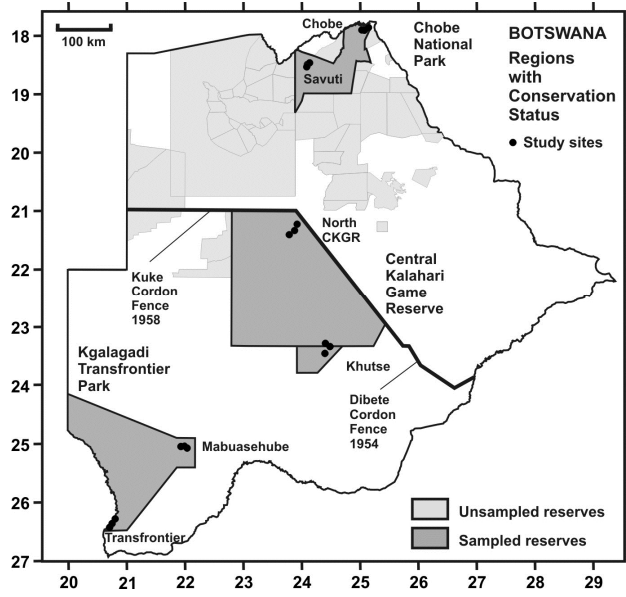


Figure 1

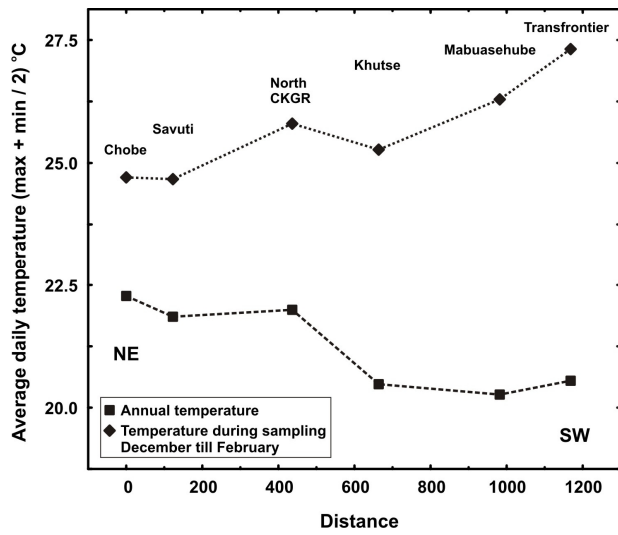


Figure 2

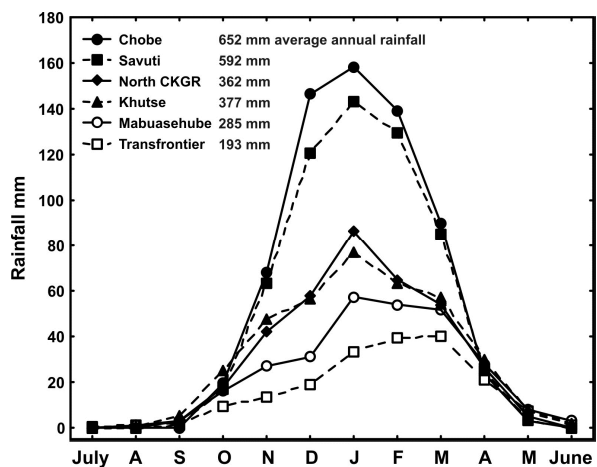


Figure 3

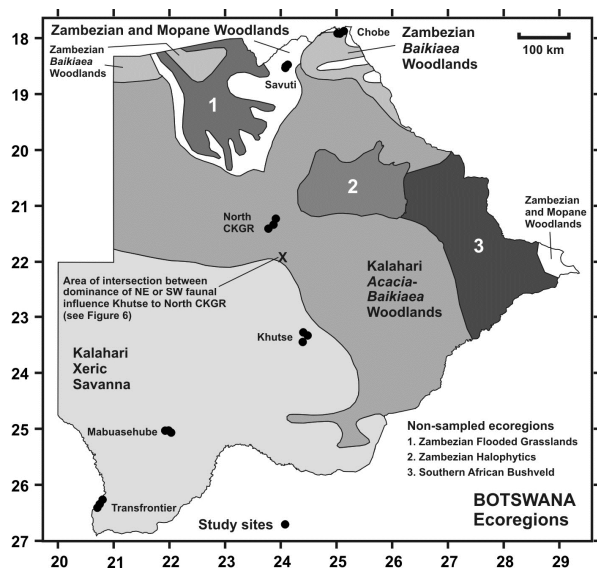


Figure 4

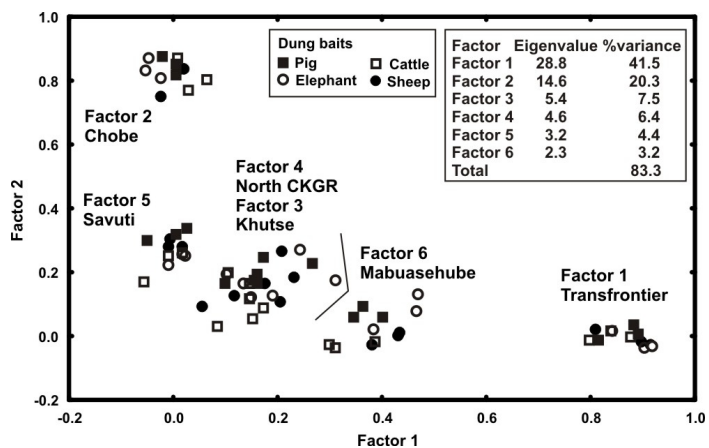


Figure 5

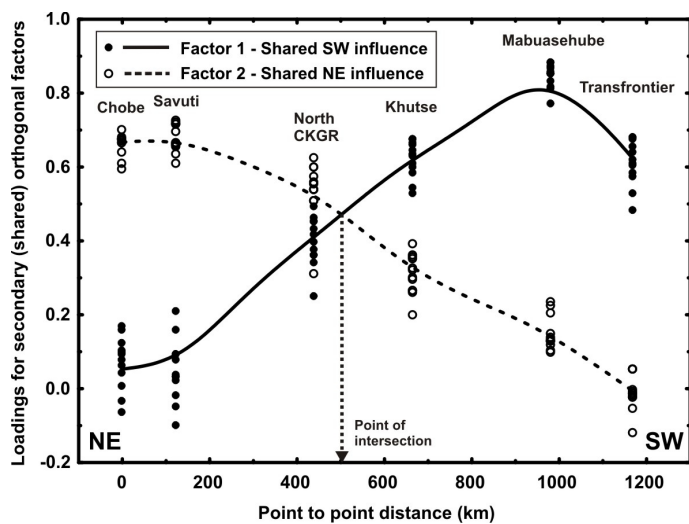


Figure 6

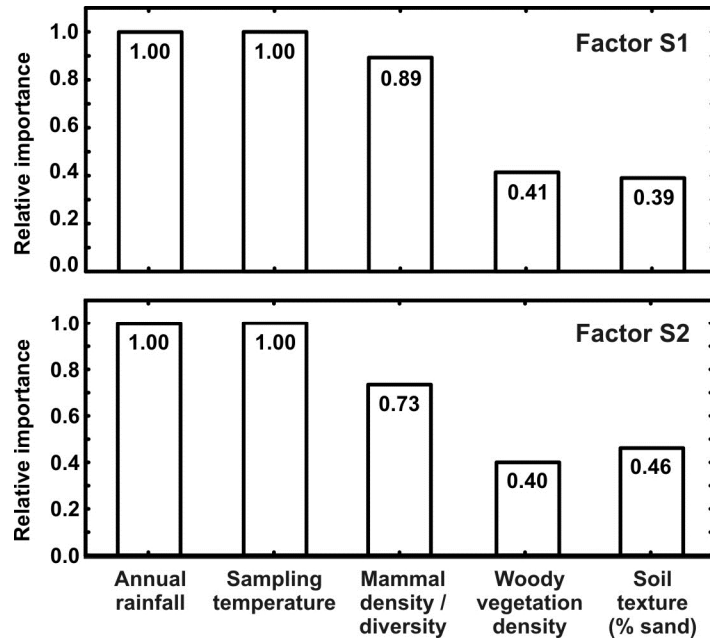


Figure 7