Does an aridity and trophic resource gradient drive patterns of dung beetle food selection across the Botswana Kalahari?

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Short title: Ecological gradients and dung beetle food selection

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Abstract. 1. Aridity gradients are paralleled by both reductions in resources and decreased species richness of animals. Across the aridity gradient of the Botswana Kalahari, reduction in mammal species richness leads to reduced density and diversity of dung types, accompanied by reduced dung beetle species richness. Would these gradients also drive changes in dung beetle food type association and specialization owing to loss of some dung types to the arid southwest?

2. Dung beetles were sampled from three study sites in each of six study areas using 2 x 10 grids of pitfall traps baited with dung (pig, elephant, cattle, sheep) or carrion (chicken livers).

3. Canonical correspondence analysis showed that distributions of dung beetle species between bait types deviated significantly from random associations.

4. Central Kalahari assemblages were more specialist than those at the mesic and arid extremes of the gradient.

5. Patterns of selection and specialization to bait types differed between mesic northeast and arid southwest study areas. There were specialist faunas on carrion and more generalist faunas on ruminant herbivore dung (cattle, sheep) in each region. However, specialist associations with elephant dung in the northeast were replaced by a more generalist fauna in the southwest with an opposite trend on pig dung.

6. Reduced species richness and high species turnover from the mesic northeast to the arid southwest is paralleled by a shift in patterns of food association that may reflect changes in the diversity of food types, particularly the absence of elephant dung from the southwest.

Key words: Aridity gradient, Botswana, dung beetle, food selection, Kalahari, Scarabaeinae, specialization, trophic gradient

Introduction

In warm temperate and tropical regions, gradients in decreasing rainfall are a limiting factor on available resources leading to lower availability of energy and reduced species richness of both plants and animals (Hawkins *et al*., 2003). Hawkins *et al*. (2003) suggest that for invertebrates such as insects, reduced rainfall results in reduced primary productivity which, in turn, limits food availability. Irrespective, of the validity of this suggestion, insect assemblages are influenced not only by quantity but also by quality of different food resources, which may provide differing combinations of plant nutrients in the case of plant-associated insects (Joern *et al*., 2012) or differing suites of dung nutrients and dung volatiles in the case of dung-associated insects (Dormont *et al*., 2010). As many plant-associated (Ward *et al*., 2003; Dennis *et al*., 2011) and dung-associated insects (Cambefort, 1982) show specialized associations with particular food types, reduced diversity and diminished availability of food across an aridity gradient would be expected to result in both associational (patterns of specialization / generalization) as well as compositional changes (species richness) in insect assemblages. The present study tests this hypothesis by comparing the dung beetle faunas of a single large arid and three mesic ecoregions (Olson *et al*., 2001) of the Botswana Kalahari across which woody plant species richness declines steeply from >200 species in the northeast to <15 species in the southwest (O'Brien *et al*., 1998). In particular, it examines if this aridity gradient drives changes in specialization and patterns of dung beetle trophic associations with carrion and different types of mammalian dung as well as reductions in their species richness.

The Botswana aridity gradient (>600 to <200 mm rain p/a) extends from northeast to southwest across the deep sand basin that covers central southern Africa. This macro-ecological setting has an origin in Miocene to Pliocene deposition of sand (Haddon & McCarthy, 2005), Pliocene development of dryer climate towards the southwest of Africa (Tyson, 1986), and Pleistocene dune development (Stokes *et al*., 1998). At the current time, large mammal species richness (19 to 14), density (4.61 to 1.93 individuals / km^2), and biomass (5881.3 to 455.9 kg/km^2) decrease across this gradient (Ministry of Environment, Wildlife & Tourism, 2004; Botswana Central Statistics Organisation, 2005; Tshikae, 2011; Tshikae *et al*., unpublished) in such a way that it leads to a reduction in diversity, density and amounts of dung to the southwest.

Dung may be classified into four major types according to physico-chemical characteristics (Davis & Scholtz, 2001) that are largely consistent with differences in mammal body size, diet, and digestive system. These comprise coarse-fibred droppings of large-bodied monogastric herbivores comprising collections of large boluses (e.g. elephants, horses), large fine-fibred pads dropped by large-bodied ruminant herbivores (e.g. buffalo, cattle), collections of small pellets dropped by mostly smaller-bodied ruminant and other herbivores (e.g. antelope, sheep, rabbits), and small, often nitrogen-rich droppings of smaller-bodied omnivores and carnivores (e.g. many primates, dogs, pigs). All four of these dung types are represented in the northeast of Botswana but only two in the southwest since large monogastric and large ruminant herbivores, are restricted to the well watered northeast region (Smithers, 1983; Skinner & Chimimba, 2005) so that pellet-dropping herbivores and carnivores dominate mammal faunas to the arid southwest (Tshikae, 2011) although they are represented across the entire region.

Decreasing mammal density and reductions in amounts and diversity of food types would have a direct effect on associated dung beetle assemblages, which not only show decreases in species richness, alpha diversity, and abundance but, also, high species turnover (beta diversity) across the Botswana aridity gradient (Tshikae, 2011; Tshikae *et al*., unpublished). These changes in dung beetle assemblage structure could be variously driven by interactions between increasing aridity and diminishing trophic resources that include interactions between both quality and quantity of available food types.

It is difficult to separate the effects of changing climate from those of changing food type availability. Both could play a part in defining a major boundary zone in the central Kalahari that separates the dung beetle fauna of the Kalahari Xeric Savanna (Olson *et al*., 2001), dominated by elements with an arid southwest Kalahari centre of biogeographical distribution (Tshikae, 2011), from those of the three northeast ecoregions dominated by dung beetles with mesic northeast or widespread patterns of biogeographical distribution. Patterns of increasing endemism with increasing aridity in the southwest Kalahari (Tshikae, 2011) are similar to those shown for dung beetles with increasing aridity in the southeast of the Iberian Peninsula where there are many species adapted to the exploitation of dry pellets (Verdú & Galante, 2002). Thus, both replacement of species of mesic climate by those better suited to arid climate and species specialization to particular dung types may be important factors in driving changes in the character of dung beetle assemblages across aridity gradients.

Dung beetles show a range of associations with regards to food type quality varying from relatively generalist to comparatively specialist (Estrada *et al*., 1993**;** Davis, 1994; Martin-Piera & Lobo, 1996; Larsen *et al*., 2006; Tshikae *et al*., 2008; Davis *et al*., 2010). Therefore, one might expect changes in ecological attributes of assemblages related to changing availability of particular dung types or limitations on regional spatial distribution of specialists according to availability of preferred dung types. Whereas dung type generalists are more likely to be limited by climatic factors, those that visit pellets or carnivore dung may be pre-adapted if not excluded by aridity, or they could even be co-evolved in the case of arid endemics. Other specialists may be limited by both climatic factors and the disappearance of preferred dung types. For instance, trophic specialization may be responsible for a group of dung beetles mostly recorded on non-ruminant herbivore dung that is largely restricted to game reserves (Davis, 1997) in mesic savanna to which large monogastric herbivores are, now, largely restricted in southern Africa. Thus, the absence of large monogastric herbivores from the southwest of Botswana might result in the exclusion of such specialist dung beetles across the aridity gradient.

As regards to food quantity, previous experimental and monitoring studies suggest that differences in arrays of available dung types would also influence dung beetle assemblages due to interactions between dropping size, density, and gross amounts of dung. Although similar numbers of species are attracted to both small (2 mL) and large (200 mL) amounts of human faeces in Panamanian rain forest, species composition, abundance structure, and body size hierarchies differ strongly (Peck & Howden, 1984). Changes in amounts and density of food resources also influence dung beetle assemblage structure (Lumaret *et al*., 1992; Lobo *et al*., 2006). Five years after the replacement of 500 head of sheep by 100 head of cattle in southern France, amounts of available dung and dung beetle abundance had increased by 300% (Lumaret *et al*., 1992). There was also a change in the relative abundance structure of the local dung beetle assemblage although no change in species composition was recorded. From a study in an arid Spanish Mediterranean system grazed by variable numbers of pellet-dropping sheep and rabbits, Lobo *et al*. (2006) concluded that variation in density of trophic resources was a key factor in driving diversity and composition of local dung beetle assemblages. Thus, changes in dropping size, amounts, and density of droppings would be expected to influence assemblage structure across the aridity and trophic resource gradient of the Botswana Kalahari.

To examine how the Botswana aridity and trophic resource gradient influenced assemblage structure, dung beetles were sampled in six study areas within conserved regions across the Botswana Kalahari. Sampling was conducted using mostly surrogate baits (chicken livers plus pig, elephant, cattle, and sheep dung) for indigenous carrion and four different classes of indigenous dung types. Whereas all five of these food types were available in the northeast, two were absent from natural dung arrays in the centre and southwest, i.e. large monogastric and large, pad-dropping, ruminant herbivores. The aims of the study were three fold. Would (1) an experimental presentation of the same five food classes in all study areas detect a change in patterns of dung beetle trophic association across the aridity and trophic resource gradient? Would (2) the faunal response be more generalist in the centre and southwest owing to reduced diversity of available food types? Would it (3) be more specialized in the northeast where there was a greater diversity of both dung beetle species (Tshikae, 2011) and available food types? The discussion focuses on how the results may have been variously influenced by interactions between increasing aridity, reduced food type diversity, and decreasing quantities of food.

Methods

Study region and gradsect design

The study was conducted across the deep sands of the Botswana Kalahari along a northeast-southwest aridity and trophic resource gradient that results from diminishing mammal density and dung type diversity (Tshikae, 2011; Fig. 1). Dung beetles were sampled from six study areas in three conserved regions; two areas per region and three study sites per area (Fig. 1). Five different bait types were used to sample dung beetles (Dung: pig, elephant, cattle, sheep; Carrion: chicken livers). As carrion and dung are often difficult to locate in reserves, pig, cattle, and sheep dung were used, respectively, as surrogates for that of indigenous omnivores (e.g. baboons) or carnivores, and pad or pellet-dropping ruminant herbivores (e.g. African buffalo or various antelope). Elephant dung represented indigenous monogastric herbivores, and chicken livers were a surrogate for wild carrion.

Across the gradsect, average annual rainfall showed a distinct gradient from moderate amounts in the northeast (>600 mm p/a) to relatively little in the arid southwest (<200 mm p/a) (Tshikae, 2011; Fig. 1) where average daily temperatures were greater during the dung beetle sampling period in the summer rainy season (Tshikae *et al*, unpublished). These gradients were marked by a decline in mammal species diversity, density, and the diversity of their dung types (Ministry of Environment, Wildlife & Tourism, 2004; Botswana Central Statistics Organisation, 2005; Fig. 1) that is, also partly, a response to the rarity or absence of surface water in the central and southwest Kalahari (Ngwamotsoko, 1995). Thus, monogastric elephants and zebra with their large fibrous droppings and ruminant buffalo with their large moist dung pads are filtered out to the southwest as they need to drink daily (Stuart & Stuart, 2006). Mammal faunas of the central and southwest Kalahari are dominated by small herbivores that drop their dung as pellets, as well as low densities of scavengers and carnivores dropping small amounts of strong-smelling faeces (Ministry of Environment, Wildlife & Tourism, 2004; Botswana Central Statistics Organisation, 2005; Fig. 1).

Trapping methods

At each of the 18 study sites, 20 x 5 L pitfall traps (top diameter = 22 cm; depth = 17.5 cm) were emplaced in a 2 x 10 grid comprising a row either side of an access track. Each trap was separated by 50 m, following the recommendations of Larsen & Forsyth (2005). Baits were placed on traps in the order of pig dung, cattle dung, elephant dung, carrion, and sheep dung, repeated four times (Tshikae, 2011). Dung baits comprised *circa* 250 mls wrapped in thin cloth to exclude dung beetles but permit release of odours. Carrion baits comprised *circa* 100 mL of fresh cloth-wrapped chicken livers that decayed rapidly under the hot temperatures in Botswana. Baits were supported at ground level over the centre of each trap using two strong wires. In each study area sampling was conducted over 48 h on a single occasion between December 2005 and February 2006. On sampling occasions, 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 killed using water and a little detergent in the base of each trap. Samples were removed and stored in ethanol after each 24 h period. A more detailed description of the trapping method may be found in Tshikae (2011).

Data analysis

Completeness of the species record for each of five bait types at each of the six study areas (5 x 6 = 30) was predicted using EstimateS version 8.2 (Colwell, 2006). Estimates for each bait type were calculated from 50 randomizations of species data recorded over 48 h for 12 samples comprising four traps from each of three study sites per study area. Of the nine estimator methods available in EstimateS, two yielded consistent results; Bootstrap and Michaelis-Menton. Therefore, only results for these two methods are reported, here.

Patterns of association between dung beetles and bait types at each of the six study areas were determined using canonical correspondence analysis (CCA) contained in the programme, CANOCO version 4.55 (ter Braak & Smilauer, 2006). The data matrices for each study area comprised mean species abundances in four traps for each of five bait types at each of three study sites (5 x 3 = 15 pooled samples each comprising mean abundance in four traps). Species sampled in very low numbers (<3 individuals) were deleted from each species abundance matrix before data analysis (Fig. 2). Sizes of the matrices were: 50 species x 15 samples in Chobe, 56 x 15 in Savuti, 29 x 15 in North CKGR, 46 x 15 in Khutse, 30 x 15 in Mabuasehube, and 36 x 15 in Transfrontier. All abundance data were $\log_{10}$ transformed before analysis to reduce the effect of species with high abundances (ter Braak & Smilauer, 2002). Monte Carlo statistical tests were used to determine if dung beetle association patterns deviated significantly from random distribution along ordination axes. CCA both calculated statistical distances between the distribution patterns of each species and fitted vector lines to an ordination plot representing associations between species and each bait type. This was possible as CANOCO recognizes both measured and dummy (categorical) environmental variables (ter Braak, 1995; Palmer, 1993). The 15 x 15 environmental matrix of dummy variables used to fit vector lines comprised a cross-tabulation of five dung types by three study sites (n=15) in which samples were coded using “1” or “0”.

In the present study, vector lines represented the mean trajectory of species associations with bait types. Differences in the angular relationship between trajectories in each of the six study areas represented differences in patterns of trophic resource partitioning. Differences in the relative lengths of vector lines represented the degree of specialization of species to each bait type with short lines defining more generalist associations and long lines more specialist associations. To compare patterns of trophic resource partitioning between study areas, the angles between all possible paired combinations of vector lines were measured for each area. To compare relative specialization between study areas, size and scale of the six ordination plots were first standardized. Lengths of the vector lines were then measured and converted to a 0-1 scale by dividing all values by that for the longest vector line. Bray-Curtis similarity matrices were constructed from untransformed data matrices of (1) study areas by angles between pairs of vector lines (6 study areas x 6 sets of angles for each area) and (2) study areas by indices of specialization (6 study areas x 5 relative lengths of vector lines for each area). The similarity matrices were subjected to the agglomerative clustering technique, group average linking, using Primer v5.0 (Clarke & Warwick, 2001). The results were summarized as dendrograms from which clusters of study areas with similar patterns of food association were defined. ANOSIM (Clarke & Warwick, 2001) was used to test the statistical significance of differences between the clusters based on comparisons between observed and 60 (angles) or 10 (specialization) possible permutations of the data.

Patterns of specialization were also examined using niche metrics and cluster analysis of spatial and trophic data. Within each of the six study areas, the trophic niche width of each species was determined from the distribution of total numbers between the five bait types. Species niche widths were calculated using the standardized version of Levins niche metric (Levins, 1968; Colwell & Futuyma, 1971), $(1/\sum p_{ij}^{2})-1 / n-1$, in which p_{ij} is the proportional abundance of the ith species on bait type j and n is the number of bait types. Consistency of results for the mean niche width within each assemblage was examined by using several scales of deletion of less abundant species, i.e. those recorded in numbers of <3, <10 and <20. Rank plots for assemblages of species recorded in numbers of 20 or >20 were compared using slopes derived from linear regression and from cluster analysis of a data matrix comprising six study sites by niche widths the first nine species. The parametric Euclidean distances similarity coefficient was used to construct a similarity matrix from the 0-1 scale data matrix. The similarity matrix was subjected to cluster analysis using the agglomerative technique, group average linking. ANOSIM (Clarke & Warwick, 2001) was used to test the statistical significance of differences between clusters based on comparisons between observed and 15 possible permutations of the data.

The combined spatial and trophic niche width for the more abundant species was calculated from the total numbers of individuals recorded across the five bait types in both northeast and southwest regions (Supplementary Table 1). The results were used to calculate mean niche width for groups of species defined from a summary dendrogram of species distribution and associations with bait types. The dendrogram was generated from analysis of a 104 x 10 data matrix comprising 104 species recorded in total numbers of >5 across the five bait types in northeast and southwest study areas (Supplementary Table 1). The raw matrix was made dimensionally homogeneous by converting the abundance data to a percentage scale across bait types. The parametric Euclidean distances similarity coefficient was used to construct a similarity matrix from this transformed data matrix. The similarity matrix was subjected to cluster analysis using Ward's method (Statistica 10 - StatSoft, 2011), which computes differences as squared Euclidean distances (Legendre & Legendre, 1998). ANOSIM (Clarke & Warwick, 2001) was used to test the statistical significance of differences between the clusters based on comparisons between observed and 999 random permutations of the data (one exception of 462 possible permutations).

Results

Completeness of the species record

Predictions of expected species richness suggest that the species record was close to complete for most bait types in each study area (Supplementary Table 2). Greater than 85% of the species were observed in all but two instances.

Canonical Correspondence Analysis (CCA)

CCA ordination plots for species / bait type associations in the six study areas are shown by Figures 2A-2F. In each case, eigenvalues for the first and second axes accounted for 46.5-62.2% of the total variance in species data and 78.8-90.8% of the total variance in species / bait type associations with relatively high correlations (Table 1). In each analysis, there was a similar clear pattern of separation along axis 1 between carrion (positive loadings for data points) and dung association (mostly negative loadings) (Figs 2A-2F). Patterns of different association between dung types were indicated by separation of species data points along axis 2. Comparative tests between the canonical axes and random (Monte Carlo) permutations detected significant patterns of association in dung beetle distribution patterns (All four axes: Chobe: F=3.75, P<0.002, axes account for 51.2% of species variance; Savuti: F=3.51, P<0.002, 63.6%; North CKGR: F=2.82, P<0.002, 45.4%: Khutse: F=3.92, P<0.002, 69.7%; Mabuasehube: F=3.53, P<0.002, 72.6%; Transfrontier: F=7.05, P<0.002, 67.2%).

Vector lines for species - bait type associations

Vector lines fitted to the ordination plots both defined and summarized patterns of species / bait type association in each study area (Figs 2A-2F). There was an angular separation of 153° to 170° between the most distant vector lines for dung types in each ordination plot, thus indicating a similar degree of maximum separation between association patterns in each study area although there was a significant imbalance between the patterns shown within the study areas ($X^2 = 639.0$, $P<0.001$; 6x6 contingency test on data in Supplementary Table 3). In northeast study areas, greatest dissimilarity was between cattle and elephant dung association (153°-157°) whereas in southwest study areas, it was between pig and ruminant herbivore dung association, either cattle or sheep dung (150°-170°) (Supplementary Table 3). Cluster analysis of data for the angle of separation between pairs of dung types showed that there were three significantly different principal patterns (ANOSIM Global R = 0.864, $P<0.017$), the mesic northeast study areas of Chobe and Savuti; the arid southwest areas of Khutse, Mabuasehube, and Transfrontier, with the pattern at the intervening North CKGR constituting an outlier (Fig. 3A, Table 2). Angular separation of pig / elephant, and cattle / sheep faunas were similarly low in both the northeast and southwest (Table 2). Angular separation of pig and ruminant dung faunas (cattle, sheep) were relatively high in both regions whereas separation between ruminant and monogastric (elephant) herbivore dung faunas were high in the northeast and much lower in the southwest where elephants do not occur (Table 2, Fig. 1).

Cluster analysis of data for proportional length of vector lines (Supplementary Table 4) generated two clusters comprising three northeast and three southwest study areas (Fig. 3B), thus indicating differences in patterns of relative generalist or specialist association with bait types between mesic and arid savanna (Table 3). Although ANOSIM comparison of clusters generated a Global R = 1 that was not statistically significant, $P<0.10$, there was a significant imbalance between the patterns shown within the study areas ($X^2 = 241.5$, $P<0.001$; 5x6 contingency test on data in Supplementary Table 4 converted to a 0-100 scale). Carrion attracted a relatively specialist dung beetle fauna in both the northeast and southwest (Table 3) as illustrated by the associations of such species as *Scarabaeus* (*Scarabaeolus*) *anderseni* Waterhouse, *Catharsius melancholicus* Boheman, and *Onthophagus apiciosus* d'Orbigny (Supplementary Table 1). Ruminant herbivore dung types (cattle, sheep) attracted a more generalist fauna in both the northeast and southwest (Table 3). Elephant dung (monogastric herbivore) attracted a more specialist fauna in the northeast as illustrated by the associations of such species as *Copris bootes* Klug, *Cheironitis indicus* van Lansberge, *Onitis orthopus* van Lansberge, and *Ixodina* sp. nr *freyi* (Janssens) (Supplementary Table 1). However, in the arid southwest where elephants do not occur, elephant dung baits attracted a more generalist fauna (Table 3). Pig dung showed an opposite trend, attracting a more generalist fauna in the northeast and a more specialist fauna in the southwest.

Niche widths and group patterns

In terms of trophic niche widths, patterns of specialization to bait types showed some variation across the Botswana aridity gradient (Fig. 4). Except for North CKGR, mean niche width within each of the six assemblages mostly showed minor increases across each of the three scales of species deletion (Table 4). At all scales of deletion, there were similar mean niche widths at the extremes of the gradsect with declines towards Khutse, which showed a consistently more specialist pattern of trophic resource partitioning. Plots of rank niche width values for species with an abundance of 20 or >20 individuals differed in slope and pattern for assemblages at the extremes of the gradsect compared to those in the boundary zone between northeast and southwest regions (North CKGR, Khutse) although the differences between patterns for the first nine species (Fig. 4 - A and B) were not significant (ANOSIM Global R = 1, $P<0.067$).

Differences in patterns of species distribution and association with bait type (Supplementary Table 1) are summarized by Figure 5. Two major clusters of species showed either northeast centres of distribution (NE bias), or southwest centres (SW bias) plus some with mixed southwest and northeast occurrence, or even northeast bias (SW4). Four clusters were defined within each major cluster and all eight were significantly different from one another (Fig. 5, Table 5 - ANOSIM Global R = 0.782, $P<0.001$). Northeast clusters (NE1-NE4) showed biases to pig dung (NE1 – 18 spp.), sheep dung (NE2 – eight spp.), or elephant dung (NE3, NE4 – 17 and six spp.) (Fig. 5). Southwest clusters (SW1-SW4) showed biases to pig dung (SW1 – 14 spp.), pig and sheep dung (SW2 – 28 spp.), or carrion comprising southwest (SW3 – eight spp.) or northeast centred species (SW4 – five spp.). Sub clusters in SW2 (Fig. 5) comprised 13 species with southwest centres and biases to pig and sheep dung (species 18, 21....52, 77); seven species occurring in both the southwest and northeast, primarily with a bias to pig dung (species 13, 28....74, 108); five southwest species mostly with a bias to elephant or cattle dung (41, 60, 84, 24, 57), and three southwest centred species with a bias to sheep dung (species 12, 59, 55).

Mean spatial and trophic niche width values for these species groups supported the analysis of specialization to bait types shown by CCA (Figs 2, 5). Elephant dung specialists were restricted to the northeast region (NE3 - 0.18; NE4 - 0.02 niche width). Specialization to pig dung was greater in the southwest region (SW1 - 0.14) than in other groups showing some bias towards pig dung association (SW2 - 0.24; NE1 - 0.21). Carrion faunas were highly specialized in both the southwest (SW3 - 0.13) and northeast regions (SW4 NE - 0.03).

Discussion

Influence of regional gradients in rainfall, surface water, and food variables

As for other rainfall gradients (Hawkins *et al.*, 2003), species richness of woody vegetation, mammals and dung beetles declined across the aridity gradient of the Botswana Kalahari (O'Brien *et al.* 1998; Ministry of Environment, Wildlife & Tourism, 2004; Botswana Central Statistics Organisation, 2005; Tshikae, 2011). These trends would be accompanied by declines in overall amounts of dung, density of droppings, and dung type diversity across the Botswana aridity gradient as large mammalian herbivores that void pads (buffalo) or large coarse fibred droppings (elephants, Burchell's zebra) and need to drink every day (Campbell, 1973; Chamaillé-Jammes *et al.*, 2007) are excluded from the central and southwest Kalahari since there is an absence of natural surface water except after rainfall (Moyo *et al.*, 1993; Penry, 1994). Over an evolutionary timescale, possibly since the Pliocene (Tyson, 1986), the increasing aridity and reduced trophic resources have resulted in a southwest Kalahari centre of endemism for dung beetles (Davis, 1997; Tshikae, 2011).

Endemism in the southwest results in a high regional turnover of dung beetle species so that largely different suites of taxa dominated species abundance patterns in the northeast and southwest (Tshikae, 2011; Tshikae *et al.*, unpublished; Fig. 5). Thus, complementary regional changes in patterns of food type association and food type specialization would be related to both the different ecological attributes of the local dung beetle assemblages and the local environmental setting. Local ecological attributes would include species richness and the relative generalization or specialization to particular food types of assemblages with differing species compositions. The local environmental setting would influence the amount, density and diversity of food types: comprising carrion, small herbivore pellets, and small carnivore droppings in the centre and southwest; and the same plus large pads and large coarse-fibred herbivore droppings in the northeast. The present study has shown that the southwest dung beetle fauna dominated by endemics (Tshikae 2011) shows different patterns of food selection and endemism to the northeast fauna. However, the suggestion that overall patterns of specialization would be greater in the northeast due to greater diversity of dung types has not been supported as mean specialization was greatest in the transition zone between the northeast and southwest regions. The reasons for this pattern are unclear.

Regional patterns of trophic resource selection

Several northeast / southwest differences in selection patterns and specialization to the same five food types have been demonstrated across the Botswana aridity gradient. Although patterns of separation between specialist, but species-poor, carrion faunas and species-rich dung faunas were consistently similar across the entire aridity gradient, there were three different patterns of dung type selection. There were also two different overall patterns of specialization to individual dung types. In the case of three food types, similar specialist (carrion) or more generalist patterns (cattle, sheep dung) were shown in both mesic and arid regions. In the case of the remaining two food types, one attracted a more generalist fauna to the southwest (elephant dung) whereas the other attracted a more specialist fauna (pig dung). The results for elephant dung demonstrate that although selectivity for dung type qualities is shown by dung beetles with extreme specialization in some northeast species, generalists may colonize any mammalian dung type to a lesser or greater extent, even if it does not occur naturally in that region as supported by results from the southwest Kalahari. The greater specialization to pig dung in the reserves of the southwest is more difficult to explain. Pig dung was used as an easily obtained surrogate for the dung of omnivores and carnivores. However, few pigs are farmed in Botswana and none were recorded in a study of indigenous mammals and domestic livestock in the southwest (Wallgren *et al*., 2008). The specialist bias to pig dung in the southwest is possibly related to the more narrow availability of dung types with a high nitrogen content dropped by local carnivores owing to the absence of omnivore baboons and vervet monkeys that are restricted to the northeast.

It seems that the between-region differences in dung type selection were related primarily to the absence of elephants (and other monogastric herbivores) from the arid southwest and the subsequent rarity of dung beetles with a strong bias to association with elephant dung. In the southwest, only *Copris cassius* Péringuey and *Metacatharsius* sp. showed a bias to elephant dung baits compared to 23 northeast dung beetle species showing group biases to elephant dung association. In the presence of such relative specialists, the northeast elephant dung faunas were more distant in composition from those attracted to other herbivore dung types than they were from those attracted to pig dung (North CKGR excepted), However, in the absence of such specialists, the southwest elephant dung fauna was more or less equidistant in composition between the faunas attracted to pig dung and ruminant dung types and was more generalist in food type selection. Despite the northeast and southwest dung beetle faunas being largely composed of different suites of species, regional trends in association by non-elephant dung specialists were relatively similar, i.e. bias to carrion, pig or sheep dung. This was notwithstanding regional differences in patterns of food type association shown by some of the relatively few species that were shared in abundance between the northeast and the southwest. There were also some within region shifts in trophic associations of individual species between local study areas. For instance, *Scarabaeus proboscideus* Guérin showed a strong bias to pig dung in Khutse and a strong bias to sheep dung in Mabuasehube and Transfrontier.

Although there were consistently different patterns of trophic specialization in three southwest and three northeast study areas, patterns of food selection in North CKGR diverged from those in two northeast study areas and from the different group pattern in the southwest. The main difference resulted from the pig dung fauna, which unlike any other study area, was close in composition to that attracted to ruminant herbivore dung. The reasons for this pattern are unclear. Annual rainfall and mammal dung type diversity were similar to Khutse to the southwest but the pattern of dung type specialization in North CKGR was closer to that in the northeast in Savuti and Chobe. Landscape factors and mammal distribution in the study area may have been influential since the study sites were placed on isolated dunes within an extensive matrix of calcrete pans where the herbivorous mammals were observed to concentrate to graze the short grass cover. The status and density of the local carnivore fauna is unknown.

Although clear group average bias has been demonstrated in food type associations, these are generalizations since many of the species were attracted in abundance to a range of food types and relative abundance patterns between bait types for individual species were not always consistent between study areas. These points must be kept in mind when making any dissection of numbers of species showing particular overall bias in spatial and trophic associations. However, a simple breakdown of numbers for the 104 most abundant species yields 23 species showing a group bias to northeast occurrence and elephant dung; seven species with a bias to pig dung association and dual abundant occurrence in the northeast and southwest; and 38 southwest or 31 northeast species biased to association with carrion, pig, or sheep dung. The five remaining southwest species were exceptional in mostly showing a bias to elephant or cattle dung. These species association patterns may reflect greater dung type diversity in the northeast whereas the roughly similar numbers of species with a bias to carrion, pig, and sheep dung in the northeast and southwest might reflect the similar availability of food types that are in common between these regions (carrion, indigenous carnivore faeces, indigenous ruminant herbivore pellets). Trophic associations and reduced species richness across the aridity gradient may, thus, parallel reduced food type diversity. However, much further supporting work is required.

Mechanisms of food selection

Dung beetles have long been considered to locate their food through olfaction (Halffter & Mathews, 1966) and there is some limited support for the selective sensory response of dung beetles to different dung volatiles (Shibuya & Inouchi, 1982; Inouchi & Shibuya, 1986). Measurements of volatiles released by four dung types revealed various common or unique compounds. The profile of each dung type differed sufficiently to separate pellet-dropping ruminant (sheep) and pad-dropping ruminant (cattle) from monogastric herbivore (horse) dung along one ordination axis with an omnivore dung type (wild boar) separating along a second axis (Dormont *et al*., 2010). Selective responses to some of these different volatiles presumably drive the range of generalist or specialist attractions to different food types that have been widely documented for various dung beetle species (Fincher *et al*., 1970; Cambefort, 1991; Davis, 1994, Martin-Piera & Lobo, 1996; Tshikae *et al*., 2008). Such variability was presumably responsible for the changes in patterns of dung type selection across the Botswana aridity gradient and contributed to the richness of overlapping dung faunas comprising a total of from 88 to 106 species on each dung type. In comparison, despite their clear differences to dung faunas, carrion faunas were less diverse (59 species) with a limited number of specialists, which could be associated with a lower diversity of volatiles released by carrion.

It is difficult to separate the effects increasing aridity, quality and quantity of food. In northeast study areas, diversity of dung types is high, comprising big to small droppings in high density resulting in large amounts. Southwest and central study areas show low dung type diversity comprising only small droppings in greater density than in the northeast but in much smaller amounts. Across this gradient, reduced diversity of dung types is paralleled by almost complete faunal turnover, reduced species richness, and changes in patterns of dung selection. It is unclear if reduced amounts of dung have also influenced these patterns. However, it is likely that reductions in amounts would be responsible for the lower dung beetle abundances recorded in the southwest compared to the northeast (Tshikae, 2011) since increasing the amounts of ruminant herbivore dung in an agro-ecosystem are known to increase the abundance of the dung beetles fauna (Lumaret *et al*., 1992).

Within each study area, the recorded dung beetle assemblage reflects the both the local array of available dung types and their responses to baits on pitfall traps, irrespective of whether or not those bait types are represented in the local array. Although dung volatiles act as attractants, they reflect different mammal diets and digestive types that result in differences in water, fibre, and nutrient content of dung. Considering the challenges of breeding in fairly dry, fibrous dung of monogastric herbivores compared to breeding in moist pads of ruminant herbivores, selection for breeding could be narrower than that for food. However, it is considered that the present records of selectivity fairly reflect faunal specialization or generalization, irrespective of whether the attraction was for feeding or breeding purposes.

Effects of ecosystem modification and conclusions

This study on dung beetles was intended, in part, to examine their responses to an experimental presentation of dung types not dropped by the indigenous mammal fauna of the southwest Kalahari. These missing dung types comprised large pads dropped by ruminant herbivores and large coarse-fibred droppings of monogastric herbivores. However, in recent decades, borehole water has permitted the support of ruminant pad-dropping cattle and monogastric equines (horse, donkey) in farmed areas and villages adjacent to conserved study areas in the southwest (Wallgren *et al*., 2008). Although some recent incursions of domestic livestock into reserves have been recorded (Ministry of Environment, Wildlife & Tourism, 2004), it is unlikely that they caused any undue bias to the present results as study sites were within reserves >20-25 km from settlements, beyond which unattended livestock are not observed (Wallgren *et al*., 2008). Wallgren *et al.* (2008) also found that at distance from both pans and villages, mammal abundance was dominated by indigenous taxa (99.8%).

In conclusion, the unmodified part of the Botswana aridity gradient is characterized by reduced mammal density and declining dung type diversity that results in a parallel trophic resource gradient. These gradients drive decreasing dung beetle species richness and high species turnover that are accompanied by changes in the patterns of association and specialization to food type.

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References

Botswana Central Statistics Organisation (2005) *Wildlife status report*. Government Press, Gaborone, Botswana.

Cambefort, Y. (1982) Les coléoptères Scarabaeidae *s. str.* de Lamto (Côte d'Ivoire): structure des peuplements et rôle dans l'écosystème. *Annals de la Société Entomologique de France*, **18**, 433–459.

Cambefort, Y. (1991) Appendix B.9(1). Pages 388-393 in I. Hanski and Y. Cambefort, editors. *Dung beetle ecology*. Princeton University Press, Princeton, USA.

Campbell, A.C. (1973) The national park and reserve system in Botswana. *Biological Conservation*, **5**, 7-14.

Chamaillé-Jammes, S., Valeix, M. & Fritz, H. (2007) Managing heterogeneity in elephant distribution: interactions between elephant population density and surface-water availability. *Journal of Applied Ecology*, **44**, 625–633.

Clarke, K. & Warwick, R.M. (2001) *Changes in marine communities*: *an approach to statistical analysis and interpretation, 2nd edition*. Primer-E Ltd, Plymouth Marine Laboratory, UK.

Colwell, R.K. (2006) *EstimateS: Statistical estimation of species richness and shared species from samples. Version 8.* Persistent URL: http://purl.oclc.org/estimates

Colwell, R.K. & Futuyma, D.J. (1971) On the measurement of niche breadth and overlap. *Ecology*, **52**, 567–576.

Davis, A.L.V. (1994) Associations of Afrotropical Coleoptera (Scarabaeidae: Aphodiidae: Staphylinidae: Hydrophilidae: Histeridae) with dung and decaying matter: implications for selection of fly-control agents for Australia. *Journal of Natural History*, **28**, 383–399.

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

Davis, A.L.V. & Scholtz, C.H. (2001) Historical versus ecological factors influencing global patterns of scarabaeine dung beetle diversity. *Diversity and Distributions*, **7**, 161–174.

Davis, A.L.V., Scholtz, C.H., Kryger, U., Deschodt, C.M. & Strümpher, W.P. (2010) Dung beetle assemblage structure in Tswalu Kalahari Reserve: responses to a mosaic of landscape types, vegetation communities, and dung types. *Environmental Entomology*, **39**, 811–820.

Dennis, R.L.H., Dapporto, L., Fattorini, S., & Cook, L.M. (2011) The generalism-specialism debate: the role of generalists in the life and death of species. *Biological Journal of the Linnean Society*, **104**, 725–737.

Dormont, L., Jay-Robert, P., Bessière, J.-M., Rapior, S. & Lumaret, J.-P. (2010) Innate olfactory preferences in dung beetles. *Journal of Experimental Biology*, **213**, 3177–3186.

Estrada, A., Halffter, G., Coates-Estrada, R. & Meritt, D.A. (1993) Dung beetles attracted to mammalian herbivore (*Alouatta palliata*) and omnivore (*Nasua narica*) dung in the tropical rain forest of Los Tuxtlas, Mexico. *Journal of Tropical Ecology,* **9**, 45–54.

Fincher, G.T., Stewart, T.B. & Davis, R. (1970) Attraction of coprophagous beetles to feces of various animals. *Journal of Parasitology*, **56**, 378–383.

Haddon, I.G. & McCarthy, T.S. (2005) The Mesozoic-Cenozoic interior sag basins of Central Africa: the Late-Cretaceous-Cenozoic Kalahari and Okavango basins. *Journal of African Earth Science*, **43**, 316–333.

Halffter, G. & Mathews, E.G. (1966) The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae). *Folia Entomologica Mexicana*, **12-14**, 1–312.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M, Porter, E.E., & Turner, J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105–3117.

Inouchi, J. & Shibuya, T. (1986) Odour responses of the olfactory receptor cells in the dung beetles. *Chemical Senses*, **11**, 286.

Joern, A., Provin, T. & Behmer, S.T. (2012) Not just the usual suspects: Insect herbivore populations and communities are associated with multiple plant nutrients. *Ecology*, **93**, 1002–1015.

Larsen, T.H., Lopera, A. & Forsyth, A. (2006) Extreme trophic and habitat specialization by Peruvian dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). *Coleopterists Bulletin*, **60**, 315–324.

Larsen, T.H. & Forsyth, A. (2005) Trap spacing and transect design for dung beetle biodiversity studies. *Biotropica*, **37**, 322–325.

Legendre, P. & Legendre, L. (1998) *Numerical ecology*. Elsevier, Amsterdam.

Levins, R. (1968) *Evolution in changing environments*. Princeton University Press, Princeton.

Lobo, J.M., Hortal, J. & Cabrero‑Sañudo, F.J. (2006) Regional and local influence of grazing activity on the diversity of a semi-arid dung beetle community. *Diversity and Distributions*, **12**, 111–123.

Lumaret, J., Kadiri, N. & Bertrand, M. (1992) Changes in resources: consequences for the dynamics of dung beetle communities. *Journal of Applied Ecology*, **29**, 349–356.

Martín-Piera, F. & Lobo, J. (1996) A comparative discussion of trophic preferences in dung beetle communities. *Miscellania Zoologica*, 19, 13–31.

Ministry of Environment, Wildlife & Tourism (2004) *Department of Wildlife and National Parks census report*. Government Press, Gaborone, Botswana.

Moyo, S., O'Keefe, P. & Sill, M. (1993) *The Southern African Environment: Profiles of the SADC Countries*. Earthscan Publications Ltd., London.

Ngwamotsoko, K.T. (1995) Keynote address. Pages 9-20 in H. Masundire, K.N. Eyeson and S.F. Mpuchane, *Wetlands management in Botswana: Proceedings of a conference held at Kasane, 14-16 November, 1994*. WCC, Gaborone.

O'Brien, E.M., Whittaker, R.J. & Field, R. (1998) Climate and woody plant diversity in southern Africa: relationships at species, genus and family levels. *Ecography*, **21**, 495–509.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., d'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001) Terrestrial ecoregions of the world: a new map of life on earth. *Bioscience*, **51**, 933–938.

Palmer, M.W. (1993) Putting things in even better order: the advantages of canonical correspondence analysis. *Ecology*. **74**, 2215–2230.

Peck, S.B. & Howden, H.F. (1984) Response of a dung beetle guild to different sizes of dung bait in a Panamanian rainforest. *Biotropica*, **16**, 235–238.

Penry, H. (1994) *Bird Atlas of Botswana*. University of Natal Press, Pietermaritzberg, South Africa.

Shibuya, T. & Inouchi, J. (1982) Fine structure and odor responses of olfactory sensillae of the Japanese dung beetle, *Copris pecuarius* (Coleoptera: Scarabaeidae). *Japanese Journal of Applied Entomology and Zoology*, **26**, 194–195.

Skinner, D.J. & Chimimba, C.T. (2005) *The mammals of the southern African subregion*. Cambridge University Press, Cape Town, South Africa.

Smithers, R.H.N. (1983) *The Mammals of the southern African subregion*. University of Pretoria, Pretoria, South Africa.

StatSoft Inc. (2011) *STATISTICA (data analysis software system), version 10.* www.statsoft.com.

Stokes, S., Haynes, G., Thomas, D.S.G., Horrocks, J.L., Higginson, J.M. & Malifa, M. (1998) Punctuated aridity in southern Africa during the last glacial cycle: the chronology of linear dune construction in the northeastern Kalahari. *Palaeogeography Palaeocimatology Palaeoecology*, **137**, 305–322.

Stuart, C. & Stuart, T. (2006) *Field guide to the larger mammals of Africa*. Struik Nature, Cape Town, South Africa.

Ter Braak, C.J.F. (1995) Ordination. Pages 91–173 in R.H.G.Jongman, C.J.F. ter Braak and O.F.R. van Tongeren, editors. *Data analysis in community and landscape ecology.* Cambridge University Press, New York, USA.

Ter Braak, C.J.F. & Smilauer, P. (2002) *CANOCO reference manual and CanoDraw for windows user's guide: software for canonical community ordination (version 4.5)*. Micocomputer Power, Ithaca, NY, USA.

Ter Braak, C.J.F. & Smilauer, P. (2006) Canoco for Windows version 4.55 Biometris-Plant Research International, Wageningen, The Netherlands.

Tshikae, B.P. (2011) *Local and regional factors influencing dung beetle assemblage structure across an environmental gradient in Botswana*. Ph.D. thesis, University of Pretoria, South Africa. Available at: http://upetd.up.ac.za/thesis/available/etd-10192011-133622/

Tshikae, B.P., Davis, A.L.V. & Scholtz, C.H. (2008) Trophic associations of a dung beetle assemblage (Scarabaeidae: Scarabaeinae) in a woodland savanna of Botswana. *Environmental Entomology*, **37**, 431–441.

Tyson, P.D. (1986) *Climatic change and variability in Southern Africa.* Oxford University Press, Cape Town.

Verdú, J.R. & Galante, E. (2002) Climatic stress, food availability and human activity as determinants of endemism patterns in the Mediterranean region: the case of dung beetles (Coleoptera, Scarabaeoidea) in the Iberian peninsula. *Diversity and Distributions*, **8**, 259–274.

Wallgren, M., Skarpe, C., Bergström, R., Kjell, D, Granlund, L. & Bergström, A. (2008) Mammal community structure in relation to disturbance and resource gradients in southern Africa. *African Journal of Ecology*, **47**, 20–31.

Ward, L.K., Hackshaw, A. & Clarke, R.T. (2003) Do food-plant preferences of modern families of phytophagous insects and mites reflect past evolution with plants? *Biological Journal of the Linnean Society*, **78**, 51–83.

Table 1. Statistics derived from ordination (Canonical Correspondence Analysis) of dung beetle species abundance distribution between five bait types at each of six study areas in the Botswana Kalahari (see Figs 2A-2F).

Study areas	Axis 1				Axis 2				Axes 1, 2	
	Eigen values	Percentage of variation		Correlation (*r*) species / baits	Eigen values	Percentage of variation		Correlation (*r*) species / baits	Cumulative % variation	
		spp*	bait**			spp*	bait**		spp*	bait**
Chobe	0.265	35.9	70.1	0.97	0.078	10.6	20.7	0.87	46.5	90.8
Savuti	0.417	34.9	55.5	0.94	0.175	14.6	23.3	0.98	49.5	78.8
North CKGR	0.475	34.0	74.8	0.99	0.096	6.9	15.1	0.92	40.9	89.9
Khutse	0.280	45.9	65.8	0.98	0.090	14.9	21.4	0.98	60.8	87.2
Mabuasehube	0.270	52.1	71.8	0.99	0.052	10.1	13.9	0.93	62.2	85.7
Transfrontier	0.500	52.3	77.8	0.99	0.074	7.7	11.5	0.85	60.0	89.3

*% variation accounted for by species data; **% variation accounted for by species / bait relationship.

Table 2. Angular separation between pairs of vector lines (see Figs 2, 3A) representing associations between dung beetle species and dung types in each study area

Comparisons	Mean angle of separation (N° ±S.D)		
Dung baits	*Northeast study areas	*N CKGR	*Southwest study areas
Cattle/Sheep	9.0 ± 1.4	41	24.0 ±25.0
Cattle/Elephant	155.0 ± 2.8	153	68.7 ±21.4
Sheep/Elephant	146.0 ± 1.4	112	79.3 ±21.2
Cattle/Pig	122.0 ±31.1	14	146.0 ±26.2
Sheep/Pig	113.0 ±32.5	27	156.7 ±12.2
Pig/Elephant	33.0 ±33.9	139	77.3 ± 9.0

*Northeast areas: Chobe, Savuti; North CKGR; Southwest areas: Khutse, Mabuasehube, Transfrontier.

Table 3. Relative specialization of dung beetle species to five food types in northeast and southwest study areas across the Botswana Kalahari (see Figs 2, 3B) (0 = biased to generalist occurrence; 1 = biased to specialist association).

Bait	Mean specialization index ±S.D.*	
Carrion or dung	**Northeast study areas	**Southwest study areas
Carrion	1.00 ±0.01	0.99 ±0.01
Pig	0.30 ±0.13	0.88 ±0.05
Elephant	0.90 ±0.08	0.32 ±0.13
Cattle	0.52 ±0.03	0.45 ±0.18
Sheep	0.43 ±0.26	0.68 ±0.18

*Derived from relative length of vector lines in Figs 2A-2F.
**Northeast study areas: Chobe, Savuti, North CKGR;
Southwest study areas: Khutse, Mabuasehube, Transfrontier.

Table 4. Mean trophic niche widths for dung beetle species recorded in six study areas from northeast to southwest across the aridity gradient of the Botswana Kalahari after deletion of less common species at three different levels of abundance.

Study area	Mean standardized niche width ±S.D.*			Total species*		
	<3	<10	<20	<3	<10	<20
Chobe	0.37 ±0.23	0.39 ±0.22	0.40 ±0.22	50	40	36
Savuti	0.27 ±0.20	0.30 ±0.20	0.32 ±0.19	56	41	31
N CKGR	0.22 ±0.19	0.31 ±0.18	0.35 ±0.13	29	15	9
Khutse	0.19 ±0.14	0.21 ±0.15	0.22 ±0.14	46	37	30
Mabuasehube	0.35 ±0.19	0.40 ±0.17	0.40 ±0.17	30	24	22
Transfrontier	0.34 ±0.20	0.41 ±0.17	0.41 ±0.18	36	25	21

* Mean niche widths for the total number of retained species after deletion of species with a total abundance of <3, <10, or <20.

Table 5. Results for paired ANOSIM comparisons between species groups defined in Figure 5 on the basis of spatial occurrence and trophic association across the aridity gradient of the Botswana Kalahari.

Spp. group	Values for R and probability, **$P<0.01$, ***$P<0.001$						
SW2	0.209**						
SW3	0.986***	0.680***					
SW4	1.000***	0.912***	1.000**				
NE1	1.000***	0.686***	1.000***	0.998***			
NE2	0.999***	0.634***	0.998***	1.000***	0.811***		
NE3	1.000***	0.723***	1.000***	1.000***	0.834***	0.780***	
NE4	1.000***	0.917***	1.000***	1.000**	1.000***	0.999**	0.478***
	SW1	SW2	SW3	SW4	NE1	NE2	NE3
	Spp. group						

Figure legends

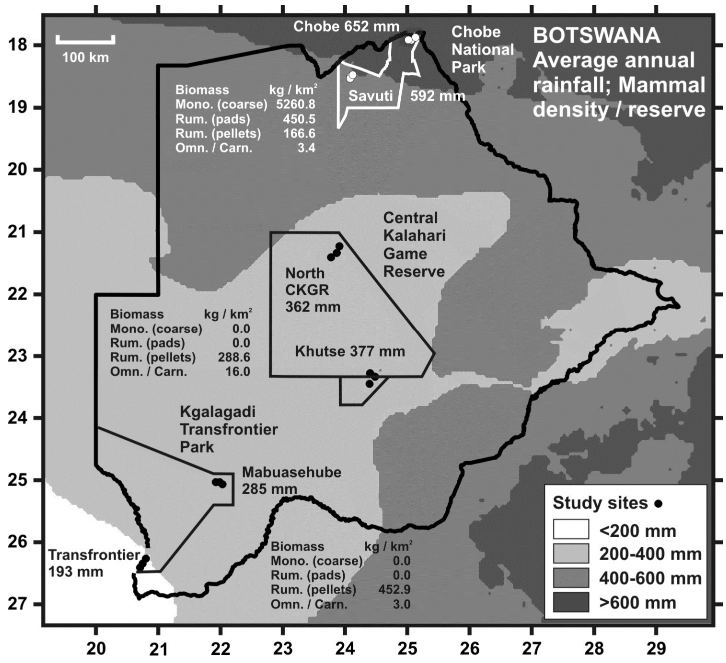
Figure 1. Annual rainfall regimes across Botswana and indigenous mammal density in three game reserves (Ministry of Wildlife, Environment & Tourism, 2004; Botswana Central Statistics Organisation, 2005) (Biomass: Mono. (coarse) = large monogastric herbivores dropping large coarse-fibred dung; Rum. (pads) = large ruminant herbivores dropping dung pads; Rum. (pellets) = ruminant herbivores dropping dung pellets; Omn. / Carn. = omnivores and carnivores dropping small, strong-smelling droppings).

Figure 2. Ordination plots showing statistical distances between associations of dung beetle species with five bait types at six study areas across the Botswana Kalahari with vector lines representing the trajectories of association with each bait type (see Supplementary Table 1 for key to species numbers). The plots are arranged according to the latitudinal gradient; left column - north to south in the northeast, right column - north to south in the southwest.

Figure 3. Dendrograms depicting: A. Similarity between patterns of association with dung types (resource partitioning); and B. Similarity between patterns of bait type specialization by dung beetle species at six study areas across the Botswana Kalahari derived, respectively, from cluster analyses of Supplementary Tables 3 or 4.

Figure 4. Rank standardized Levins trophic niche width values for species of dung beetles recorded in numbers of 20 or >20 across five bait types in six study areas across the Botswana Kalahari; slopes for linear regression on the rank values; and a dendrogram depicting similarity between the rank patterns for the first nine species.

Figure 5. Dendrogram depicting similarity between patterns of species association with bait types in northeast (Chobe, Savuti, North CKGR) and southwest study areas (Khutse, Mabuasehube, Transfrontier). Bar diagrams show average patterns of associations for two major and eight minor clusters defined, respectively, at distances of 99 and 12-20 on a 100-0 scale of linkages (see Supplementary Table 1 for key to species numbers). The y axis of the bar diagrams represents the average percentage abundance of species (uniform 0-100% scale) on five different bait types arranged along the x axis in the order of carrion, pig, elephant, cattle and sheep dung with black bars representing results from northeast study areas and grey bars representing results from southwest study areas. Mean spatial / trophic niche widths are cited in the bar diagrams for each species group (0=specialist, 1=generalist). Of the 104 most abundant species (out of 139), 80 species occurred in the northeast and 70 species in the southwest with 46 shared. There were 49 species with >85% of their abundance biased to the northeast, 38 species with a similar bias to the southwest, and 17 that were more equitably shared between regions.


BOTSWANA
Average annual rainfall; Mammal density / reserve
100 km
Chobe 652 mm
Chobe National Park
Savuti
592 mm
Biomass kg / km²
Mono. (coarse) 5260.8
Rum. (pads) 450.5
Rum. (pellets) 166.6
Omn. / Carn. 3.4
Central Kalahari Game Reserve
North CKGR 362 mm
Khutse 377 mm
Biomass kg / km²
Mono. (coarse) 0.0
Rum. (pads) 0.0
Rum. (pellets) 288.6
Omn. / Carn. 16.0
Kgalagadi Transfrontier Park
Mabuasehube 285 mm
Transfrontier 193 mm
Biomass kg / km²
Mono. (coarse) 0.0
Rum. (pads) 0.0
Rum. (pellets) 452.9
Omn. / Carn. 3.0
Study sites ●
<200 mm
200-400 mm
400-600 mm
>600 mm
18
19
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29

Figure 1.

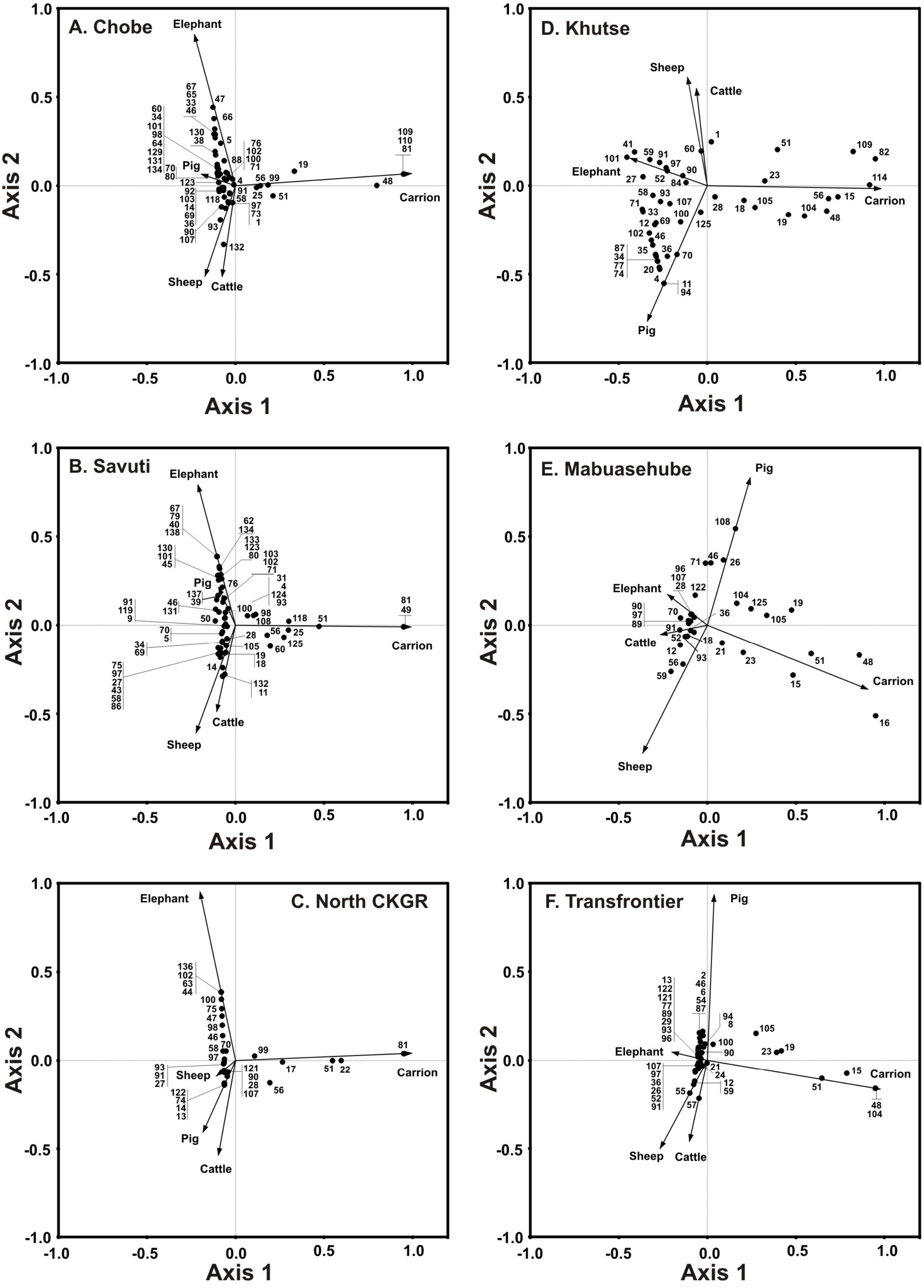
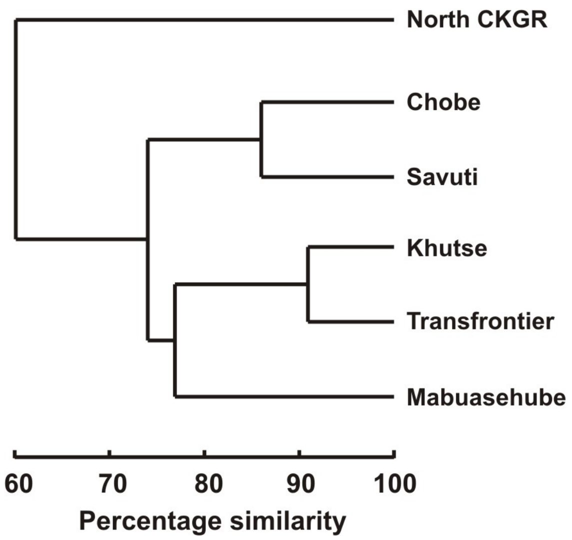

A. Chobe
Elephant
Pig
Sheep
Cattle
Carrion
67
65
33
46
47
66
60
34
101
98
64
129
131
134
70
80
130
38
5
76
102
100
71
88
109
110
81
19
123
92
103
14
69
36
90
107
118
4
91
25
58
97
73
1
56
99
51
48
93
132
D. Khutse
Sheep
Cattle
Elephant
Pig
Carrion
1
51
109
82
41
59
91
60
101
97
90
27
52
84
23
114
58
93
71
107
33
100
28
18
105
56
15
12
69
125
19
104
48
102
46
36
87
35
70
34
77
74
20
4
11
94
B. Savuti
Elephant
Pig
Sheep
Cattle
Carrion
67
79
40
138
62
134
133
123
80
103
102
71
130
101
45
76
31
4
124
93
137
39
46
131
91
119
9
50
100
98
108
118
51
81
49
70
5
28
56
25
34
69
105
60
125
19
18
75
97
27
43
58
86
14
132
11
E. Mabuasehube
Pig
108
71
46
26
96
107
28
122
Elephant
104
125
19
105
90
97
89
70
36
91
Cattle
52
18
12
21
23
51
48
56
93
59
15
Carrion
16
Sheep
C. North CKGR
Elephant
136
102
63
44
100
75
47
98
46
70
58
97
99
81
Carrion
93
91
27
Sheep
121
90
28
107
17
51
22
56
122
74
14
13
Pig
Cattle
F. Transfrontier
Pig
13
122
121
77
89
29
93
96
2
46
6
54
87
94
8
105
100
90
23
19
Elephant
107
97
36
26
52
91
21
24
12
59
55
57
15
51
Carrion
48
104
Sheep
Cattle
Axis 1
Axis 2
1.0
0.5
0.0
-0.5
-1.0

Figure 2.

A. Pattern of resource partitioning



B. Pattern of dung type specialization

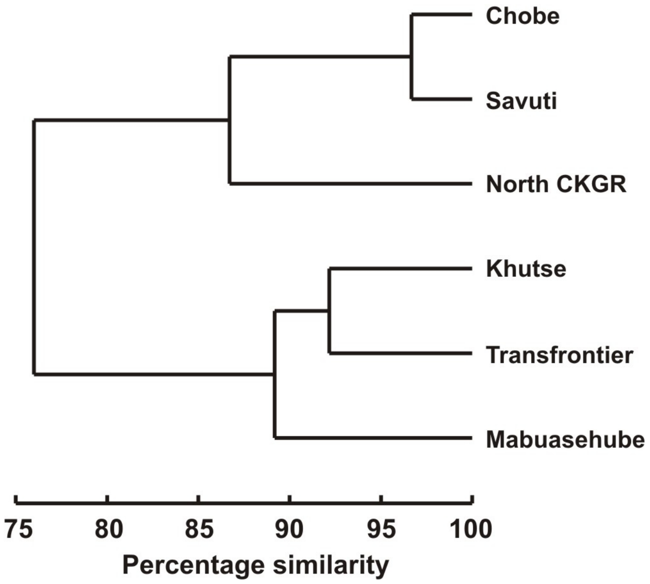


Figure 3.

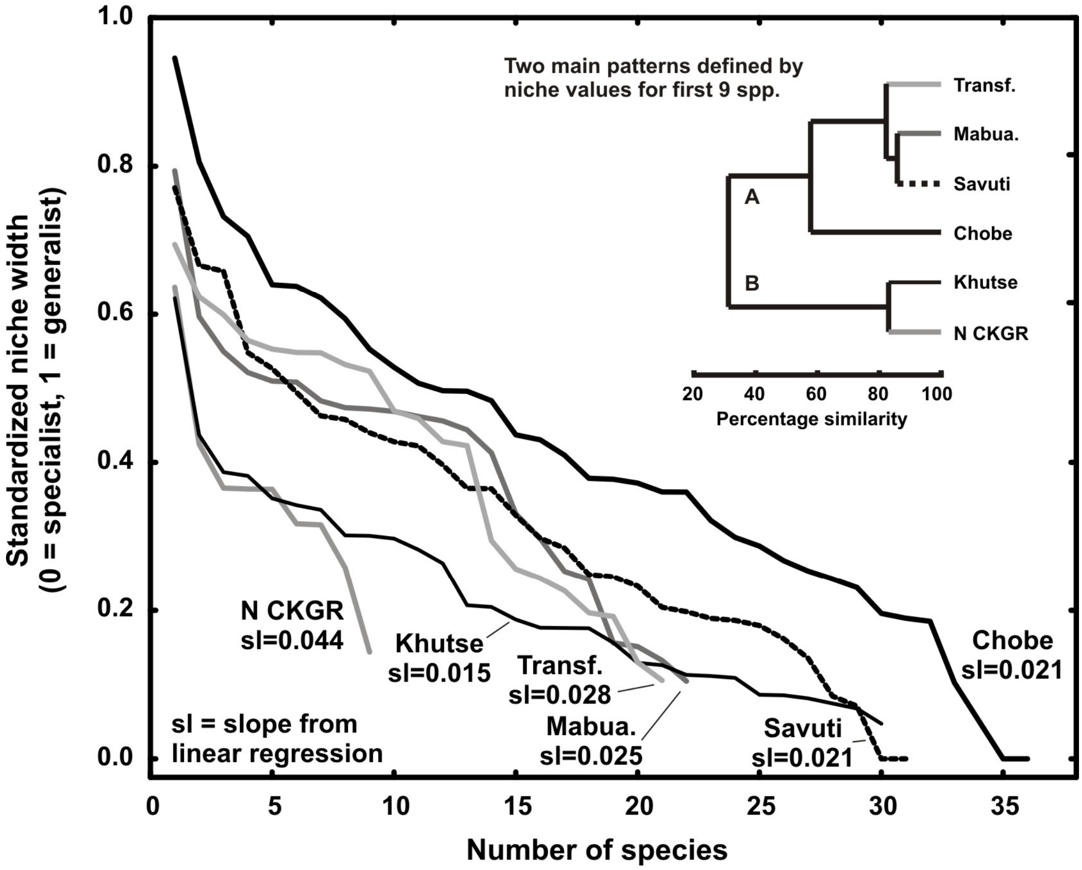

1.0
0.8
0.6
0.4
0.2
0.0
Standardized niche width
(0 = specialist, 1 = generalist)
0
5
10
15
20
25
30
35
Number of species
Two main patterns defined by
niche values for first 9 spp.
Transf.
Mabua.
Savuti
Chobe
Khutse
N CKGR
A
B
20
40
60
80
100
Percentage similarity
N CKGR
sl=0.044
Khutse
sl=0.015
Transf.
sl=0.028
Mabua.
sl=0.025
Savuti
sl=0.021
Chobe
sl=0.021
sl = slope from
linear regression

FIGURE 4.

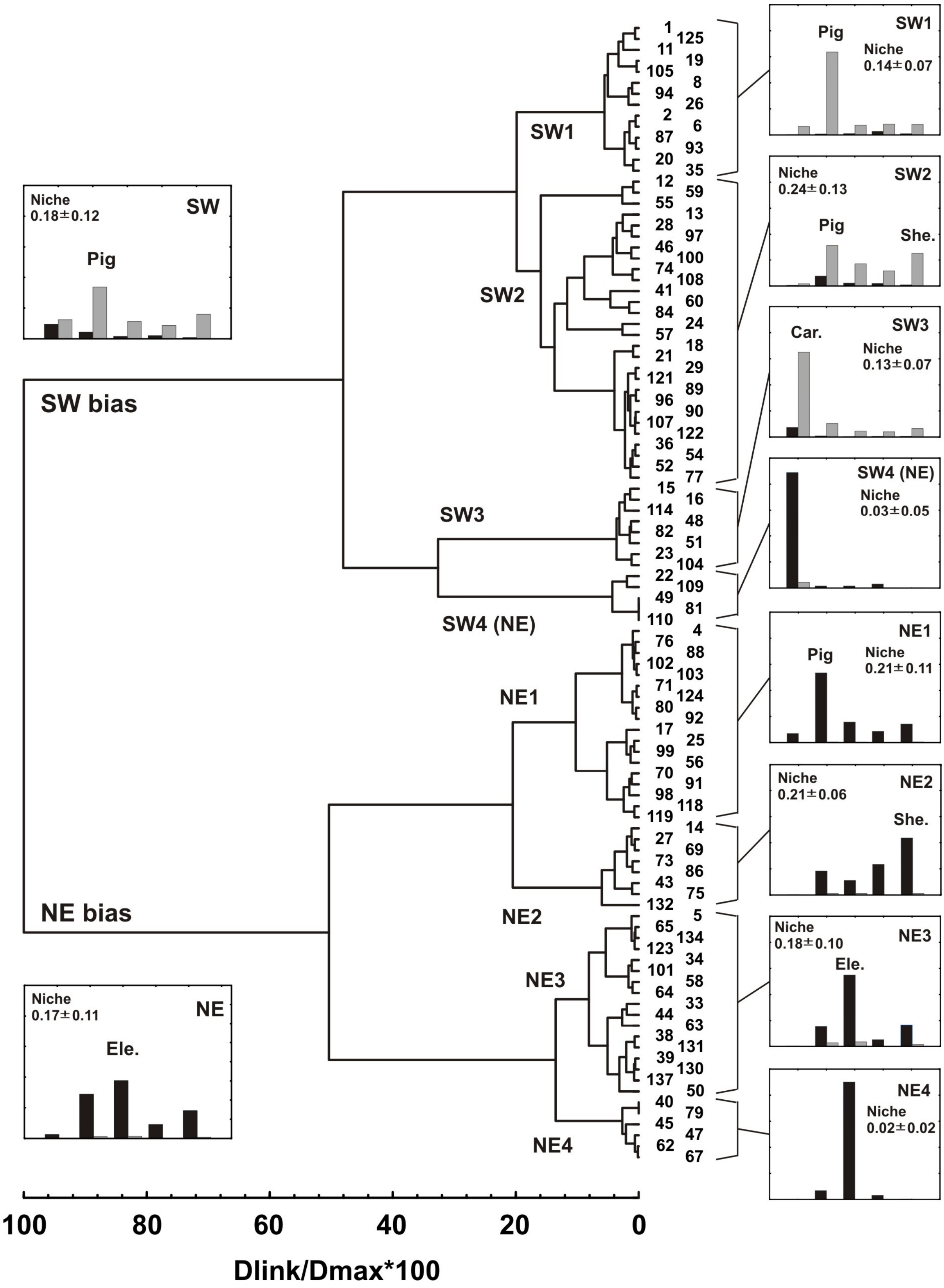

SW1
SW2
SW3
SW4 (NE)
NE1
NE2
NE3
NE4
SW bias
NE bias
Niche
0.18±0.12
SW
Pig
Niche
0.17±0.11
NE
Ele.
Pig
SW1
Niche
0.14±0.07
Niche
0.24±0.13
SW2
Pig
She.
Car.
SW3
Niche
0.13±0.07
SW4 (NE)
Niche
0.03±0.05
NE1
Pig
Niche
0.21±0.11
Niche
0.21±0.06
NE2
She.
Niche
0.18±0.10
NE3
Ele.
NE4
Niche
0.02±0.02
1
125
11
19
105
8
94
26
2
6
87
93
20
35
12
59
55
13
28
97
46
100
74
108
41
60
84
24
57
18
21
29
121
89
96
90
107
122
36
54
52
77
15
16
114
48
82
51
23
104
22
109
49
81
110
4
76
88
102
103
71
124
80
92
17
25
99
56
70
91
98
118
119
14
27
69
73
86
43
75
132
5
65
134
123
34
101
58
64
33
44
63
38
131
39
130
137
50
40
79
45
47
62
67
100
80
60
40
20
0
Dlink/Dmax*100

Figure 5.