

Dung beetle conservation biogeography in southern Africa: current challenges and potential effects of climatic change

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Abstract

Miocene, Pliocene and Pleistocene changes to the geomorphology, climate and vegetation of southern Africa are considered responsible for radical differences between southwest and northeast dung beetle assemblages (Coleoptera: Scarabaeidae: Scarabaeinae) leading to current endemism in Namibia, Botswana and South Africa. This bias is supported by distributional analysis of 437 species across vegetation regions and 2°x2° squares of latitude and longitude using non-metric multidimensional scaling (NMDS) and minimum spanning trees (MST). The ordinal values for six NMDS dimensions showed significant correlations with annual rainfall, annual temperature, rainfall seasonality and altitude. Significant climatic differences were also shown between six regional centres defined and modelled for the subcontinent: winter/bimodal rainfall, southwest arid, southeast highlands, savanna, sandy savanna and east coast. Twenty-one, principal, subregional centres defined from further NMDS and MST analyses of regional data showed significant intra-regional differences in climatic attributes although published data suggest that soil, vegetation and dung type associations were frequent additional influences. Species showing the smallest ranges were centred primarily around the coast and bordering escarpments, which coincide with regions and subregions showing unique environmental conditions characterized by many endemic genera and species. Published land use data indicate that large parts of these regions are highly transformed or degraded, so that some species are facing strong current threats. Furthermore, published global climatic change data suggest that many endemic species could be further threatened, especially to the southwest where the late Cenozoic trend to unique climatic and environmental conditions could, potentially, be reversed in the future.

Keywords Climate change · Conservation biogeography · Dung beetles · Scarabaeinae · Southern Africa

Introduction

Dung beetles have been identified as useful indicators of diversity, endemism and environmental quality in biogeographical, conservation and agro-ecosystem studies (Halffter & Favila 1993; McGeoch et al. 2002; Davis et al. 2004; Spector 2006; Nichols et al. 2007; 2008) where they are important for burial of dung, recycling of nutrients, control of dung breeding pests (Waterhouse 1974; Bornemissza 1979), bioturbation of soil (Brown et al. 2010) and dispersal of seeds (Andresen 2002). They are particularly useful as indicators in the southern African subcontinent where dung beetle species occurrence and seasonality (Davis 1994; 1997) are strongly influenced by high climatic (Walter & Lieth 1964), topographical (Partridge & Maud 1987), edaphic (FAO 2012) and vegetation diversity (Olson et al. 2001; Mucina & Rutherford 2006). Development of this environmental diversity is considered to date from the late Cenozoic (Neumann & Bamford 2015) and to be responsible for a high degree of dung beetle endemism, particularly in the winter rainfall, arid, sandy Kalahari and highland regions to the southwest and southeast (Davis 1997). Consequently, there are many current challenges for conservation of dung beetle species across southern Africa, particularly those showing the smallest overall ranges and/or those showing specialist ecological associations within areas under the greatest pressures from urbanization, resource exploitation or conversion to agro-ecosystems (Fairbanks et al. 2000; Davis et al. In press). In the southwest, additional, future conservation challenges could result from predicted climatic change (Giorgi 2006; Scheiter & Higgins 2009; Rintoul et al. 2018), particularly if it drives reversion from the present winter rainfall climate (Dieppois et al. 2016) to the earlier more tropical system (Sciscio et al. 2016) that preceded permanent glaciation in polar regions from the mid-Miocene (Zachos et al. 2001).

Across the African subcontinent south of 17° S, dung beetle species occurrence and endemism have been strongly influenced by orogenics comprising a southern mountain belt and a central plateau bordered by a predominantly narrow band of coastal lowlands that broaden to the northeast on the Mozambique Coastal Plain. Along the south to southwest coast, the lowlands are bordered by the Cape fold mountain ranges, which originate from old Triassic to Permian orogenies recently dated to 261 and 248 Ma (Hansma et al. 2016). Along the more extensive west and east coasts, escarpments delineate the tilted central southern African plateau that is higher towards the east and may represent episodic uplift of an early Cenozoic, low altitude, erosion surface (Burke & Gunnell 2008) during the early Miocene (moderate at ~18 Ma) and late Pliocene (major at ~2.5 Ma) (Partridge & Maud 1987). Although some subsequent studies question the precise chronology (Said et al. 2015, Baby et al. 2018), they all support uplift of the plateau in the late Cenozoic (Paul et al. 2014, Rudge et al. 2015), leading to a centre of dung beetle endemism in the southeast (Davis 1997).

Specificity to particular soil types (Davis 1996) is also a strong determinant of dung beetle species occurrence and endemism. Although most soils on the plateau are finer-grained sandy loams and sandy clay loams to clay loams (FAO 2012), there are also extensive areas dominated by deep sands. For the most part, these are found in a north central depression of the plateau, comprising the Kalahari Basin, or, around the coastline, particularly in the west. The Kalahari sands overlay earlier strata having been deposited by riverine erosion of sandstone (Haddon & McCarthy 2005) following the Miocene / Pliocene uplift of the Highveld and Upper Karoo to the southeast. As a result, the drier southwest Kalahari has, also, become a centre of dung beetle endemism (Davis 1997).

With regard to temperature, rainfall and rainfall seasonality, climate type is a further particularly strong determinant of dung beetle species occurrence and endemism across the subcontinent (Davis 1994, 1997). Subcontinental climatic patterns south of 17°S may be summarized as being influenced by three different cells of air currents (Neumann & Bamford 2015). (1) The easterly Indian Ocean anticyclonic system overlies the warm Agulhas Current and expands sequentially across southern Africa in summer bringing mid-summer peaks in rainfall to north South Africa, Zimbabwe and north Botswana (December / January) but late summer peaks in rainfall to the southwest in north Namibia (February) and the Northern Cape in South Africa (March) (Taljaard

1986; Dieppois et al. 2016), followed by dry winters. (2) The westerly Polar Frontal system overlies the Benguela Current and expands from the extreme South Atlantic Ocean bringing winter rainfall to the southwest tip of South Africa (Dieppois et al. 2016), followed by dry summers. Along the south coast, interplay between systems results in even rainfall or a weak bimodal spring / autumn pattern (Walter & Lieth 1964). (3) Along the west coast of southern Africa, the South Atlantic anticyclonic system comprises offshore southeast trade winds that are cool and dry due to upwelling of the cold Benguela current, leading in turn to onshore aridity (Walter & Lieth 1964) that extends far inland to the southeast between the maximum expansions of (1) and (2). Currently, endemic, cool-adapted, dung beetles in the southwest show mainly spring activity peaks (Davis 1993) that are quite different to the mid-summer activity peaks shown by warm-adapted dung beetles in the summer rainfall region to the northeast (Davis 1994).

Evolution of dung beetle endemism due to development of winter rainfall and arid climatic patterns in southwestern Africa may date from the abrupt mid-Miocene decrease in temperatures (Zachos et al. 2001) with development of permanent south polar glaciation that drove the mid to upper Miocene onset (Heinrich et al. 2011; Rommerskirchen et al. 2011) of the cold Benguela Current upwelling along the west coast of southern Africa at 11.8 Ma. In the late Pliocene, northwards shift of this upwelling paralleled cooling and expansion of Antarctic sea ice (Petrick et al. 2015). These trends were coeval with a change from humid to dry to arid climate in Namibia (Diekmann et al. 2003) resulting in a transition from woodland to grasslands to arid vegetation between 9-2.7 Ma (Hoetzel et al. 2015).

Fossil diatom evidence suggests temperature-driven movements of the Polar Front across 20° of latitude between the mid-Miocene to present (Cervato & Burckle 2003). Movement to the north may have led to inception of winter rainfall climate in southwest South Africa during the Pliocene (± 3 Ma) (Deacon 1983) although dry summers may have occurred from the late Miocene onwards (Linder 2003). Nevertheless, northwards expansion of the Polar Front is suggested to be linked to a period of intensification of winter rainfall climate during the late Pliocene (Diekmann et al. 2003). Parallels have also been reported between the increased extent of Antarctic sea ice and enhancement of winter rainfall climate during the Quaternary (Stuut et al. 2004). Climatic change in the southwest Cape is supported by biogeochemical and palynological evidence for early to mid-Miocene subtropical climate (Sciscio et al. 2016) followed by late Miocene (10-6 Ma) transition from tropical to semi-arid vegetation (Dupont et al. 2011).

The geomorphological and climatic evolution is largely responsible for the current delineation of biomes (Mucina & Rutherford 2006; Bergh et al. 2014) and ecoregions (Olson et al. 2001). These are dominated by different natural vegetation types that are of great importance for dung beetle habitat associations (Davis 1993; 1996a; Davis et al. 2002). The Fynbos, Renosterveld and Succulent Karoo comprise shrublands with patches of forest and coincide with the winter and bimodal rainfall regions in the southwest and south of South Africa. In the arid late summer rainfall system of the Namib Desert and Nama Karoo (Walter & Lieth 1964, Mucina & Rutherford 2006, Olson et al. 2001), arid grasslands and shrublands extend from the west Namibian coast into the southwest centre of the subcontinent. In the mid-summer rainfall region, the southeast highlands are dominated by grassland whereas the northeast and east of southern Africa are variously covered by grasslands, woodlands or forest of the Savanna and Indian Ocean Coastal Belt. The most southerly vegetation regions are largely restricted to southern Africa with only the eastern coastal system and savanna continuing into the tropics (Neumann & Bamford 2015).

The present study has three major aims. (1) It first analyzes the spatial distribution patterns of 437 dung beetle species across southern Africa, thus, updating an earlier study (Davis 1997). (2) It then discusses how dung beetle biogeography and endemism has been influenced by current geomorphology, climate, vegetation and edaphic characteristics that are considered to have evolved primarily since the mid-Miocene (Neumann & Bamford 2015). (3) The findings are then discussed with regards to current challenges for regional conservation

of dung beetles due to habitat transformation (Fairbanks et al. 2000) as well as future potential impacts of climatic change that have been predicted for the subcontinent (Giorgi 2006; Scheiter & Higgins 2009; Rintoul et al. 2018).

Methods

Data set

Distribution data were derived from a database (available at <http://vmus.adu.org.za/>) and both published and unpublished field records of the Scarab Research Group, University of Pretoria (see maps in Davis et al. In press). Selected scarabaeine dung beetle species are those recorded in South Africa, Botswana and Namibia for which more or less validated names are available. Distribution data for these 541 species were plotted across a map panel extending from 17-35° S and 11-33° E in southern Africa. This delimits the three target countries plus most of Zimbabwe, the extreme southwest of Mozambique and, also, the extreme south of Angola and Zambia. Species recorded in the non-target countries, but not in South Africa, Botswana or Namibia, were not considered.

Distributional data matrices

Nine species data matrices were developed across a hierarchy of three spatial scales. Analysis of a single subcontinental data matrix generated six regional species clusters. Analyses of the six regional data matrices generated 28 subregional species clusters. Two subregional data matrices were further subdivided by analyses so that there was a final total of 31 subregional species clusters. Each data matrix comprised the number of 1/16th degree squares occupied by each species within both vegetation regions (biomes or ecoregions) and 2°x2° squares of latitude and longitude across the map panel.

For each species at subcontinental scale, the combined data matrix comprised: (1) numbers of occupied 1/16th degree squares within each of seven biomes of South Africa (Mucina & Rutherford 2006; savanna split into Kalahari and bushveld subunits; no data for desert or forest biomes); (2) numbers of occupied 1/16th degree squares within each of 13 ecoregions defined for the remainder of the map panel (Olson et al. 2001; no data for three saline pan ecoregions) and (3) numbers of occupied 1/16th degree squares within each of 86, 2°x2° squares of latitude and longitude within the map panel. Ultimately, this matrix comprised distribution data for 437 dung beetle species across 107 spatial divisions after a total of 95 deletions of poorly-known species from four range size categories and deletions of a further nine species whose status was taxonomically uncertain. Four scales of deletion were chosen based on the overall size of each species range within Africa (see Extents of Occurrence (=EOO) in Davis et al. In press). The smallest range scale was, A: 2×10^4 km² (20,000 km²), which is the spatial limit at which species threat categories (Ex, CR, En, Vu, NT) are defined by the IUCN (IUCN 2001). The remaining range scales were, B: 2×10^4 to 10^5 km², C: 10^5 to 10^6 km² and D: $>10^6$ km². As many species showed genuinely small ranges that were not collecting artefacts, only species occurring in <2 , 1/16th degree squares were deleted from category A (Table S1). The remaining levels of deletion were: B: <7 , C: <12 , and D: <17 , 1/16th degree squares.

The data matrices constructed for six regional and two subregional species clusters varied in size according to numbers of representative species and numbers of occupied spatial divisions. For each of these eight data sets, matrix size is specified on figures depicting each ordination plot from which subregions are defined.

A data matrix was also developed for the 67 genera included in the subcontinental scale analysis that assigned each of 437 species to one of six regional centres of distribution. Thus, in this 67 x 6 matrix, data represented numbers of species centred on each region for each genus.

Distributional data analyses

Each of the nine species data matrices was analyzed using an adaptation of non-metric multidimensional scaling (NMDS) contained in the statistical package, Statistica vers. 13.3 (TIBCO Software Inc. 1984-2017). Each raw data matrix was first converted to a correlation matrix. Because each matrix would be expected to be strongly influenced by the differing regional effects of annual temperature, annual rainfall, rainfall seasonality, altitude and habitat (soil and vegetation) (Davis 1996a, 1997; Tshikae et al. 2013a; Davis et al. 2014, 2016), six dimensions (=ordination axes) were specified for each NMDS analysis. Firstly, the non-metric, Standard Guttman-Lingoes method (See Shiffman et al. 1981) extracted what amounts to principal components across six dimensions as a starting configuration. Secondly, the Kruskal steepest descent algorithm (Kruskal 1964) monotonically ranked similarities or distances between correlation values to achieve an optimal configuration by a process of iteration (set at the default of minimum 6, maximum 50 iterations). At each step, the steepest descent algorithm determined the least raw stress in configuration and was followed by up to five further iterations that minimized the standardized stress for precision of results. Iterations of ranking to determine the least raw and standardized stress were continued until a solution (convergence) was achieved. The smaller the stress value, the better the fit of the reproduced distance matrix to the observed distance matrix. (See Kruskal 1964; Shiffman et al. 1981).

The generic data matrix was also analyzed using non-metric multidimensional scaling (NMDS) although, at this higher taxon level, five dimensions were specified for analyses. The analysis examined similarities and dissimilarities in the centring of the 67 genera across the southern African subcontinent.

Minimum spanning trees

Minimum spanning trees were fitted to each NMDS ordination plot for dimensions 1 and 2 using the distance matrix, which comprised total distances across all six (species level analyses), or, all five dimensions (generic level analysis). Distance values between each genus or species pair were first placed in rank order. Using this ranked distance matrix, a search then determined the shortest distances between each generic or species pair. Searching continued until all generic or species data points were connected by a complete tree comprising minimum distances.

Clusters of genera and species with similar geographical distribution were defined from the distribution of data points in ordinal space assisted by the manner in which they were connected by a minimum spanning tree. For each ordination, a distance was selected below which data points were joined by a solid line and above which more distant data points were connected by a dotted line. Although this was designed to assist division into geographical groups, in practice, species clusters were often less well-defined than ideal. This was due primarily to two factors. One was amplification of distances between species with similar distribution centres but large differences in numbers of occupied 1/16th degree squares. The other was reduction of distances due to the degree of range overlap between species that otherwise showed different centres of distribution, particularly in the moister, warmer northeast of the subcontinent.

Regional and subregional distribution maps

Using data points representing 1/16th degree squares, distribution of each regional and subregional cluster comprising >3 species was plotted on the 17°-35° S by 11°-33° E map panel for southern Africa. Combined distribution of species with ranges <20,000 km² was also plotted on the map panel. Because of the extensive overlap between distribution patterns, each occupied 2°x2° square of latitude and longitude was shaded to represent quartile proportions of total species numbers for each group. This classification of species numbers in each square clearly demonstrated the different centres of distribution.

Distributional modelling

Biomapper 4 (Hirzel et al. 2007) was used to model combined ranges of species represented in each of the six regional centres. Each 5x5 km polygon for which there were records was weighted according to the number of species present. Modelling was based on GIS maps for (1) the amount and (2) seasonality of annual rainfall (% between November and March) and (3) mean annual daily temperature (max.+min./2) in 5x5 km polygons across Africa (see ranges within map panel for southern Africa in Figs S1A-S1D). The maps were Box-Cox transformed and standardized. Three factor maps were first produced by Ecological Niche Factor Analysis (ENFA). A habitat suitability map was then produced from the factor maps using the geometric mean algorithm. Habitat suitability has been presented as four ranges of probability for the target area in southern Africa (0-25%, 25-50%, 50-75%, 75-100%).

Environmental data and analyses

For each of 437 species, spot distribution data across southern Africa south of 15° S were used to extract environmental data from GIS base maps. These maps comprised average values in 5x5 km polygons for altitude, annual rainfall, annual daily temperature (max.+min./2) and rainfall seasonality (proportion of annual rainfall falling between November and March) (see ranges within map panel in Figs S1A-S1D). As numbers of observations differed between taxa, average values were first calculated for each species (Davis et al. In press). Using these average values, Spearman Rank Correlations were used to test for correlation between the four environmental variables and the ordinal values for each of the six dimensions generated by the NMDS analysis at subcontinental scale. Mean values and a standard deviation for environmental variables were also calculated for each regional and subregional species group that comprised >3 species. Kruskal-Wallis ANOVA tests (Statistica vers. 13.3, TIBCO Software Inc. 1984-2017) were conducted to determine if values for each environmental variable differed significantly between the six regions defined from NMDS analysis of species data. Further Kruskal-Wallis tests determined if environmental variables differed significantly between subregions within four of the six regions. For each Kruskal-Wallis test multiple comparisons of mean ranks were conducted to determine which values contributed to significant differences.

Results

Regional biogeographical patterns

Six regional clusters were defined from NMDS ordination of distributional data for 437 dung beetle species within the subcontinent of southern Africa (Fig. 1). These clusters were centred on: (1) the winter and bimodal rainfall region along the west and south coast of South Africa (Fig. 2A); (2) the southwest arid region extending northwest from central South Africa to the Namibian coast (Fig. 2B); (3) the southeast highlands of South Africa (Fig. 2C); (4) the savanna (Fig. 2D) and (5) sandy savanna regions of north and northeast southern Africa (Fig. 2E); plus (6) the east coast of southern Africa (Fig. 2F). The generalized regional bias of these distribution centres was supported by modelling (Figs 3A-3F).

Twelve clusters were defined from an ordination biplot that analyzed distribution of 67 genera according to how their species were centred across the six regions (Fig. 4; Table S2). A total of 17 genera showed a southwest or southeast bias in distribution (Groups 1-5) whereas the remainder showed a northeast bias (Groups 6-10 and 11-12). Of the 50 genera showing a northeast distributional bias, only 10 contributed a few species that were centred in the winter and bimodal rainfall regions.

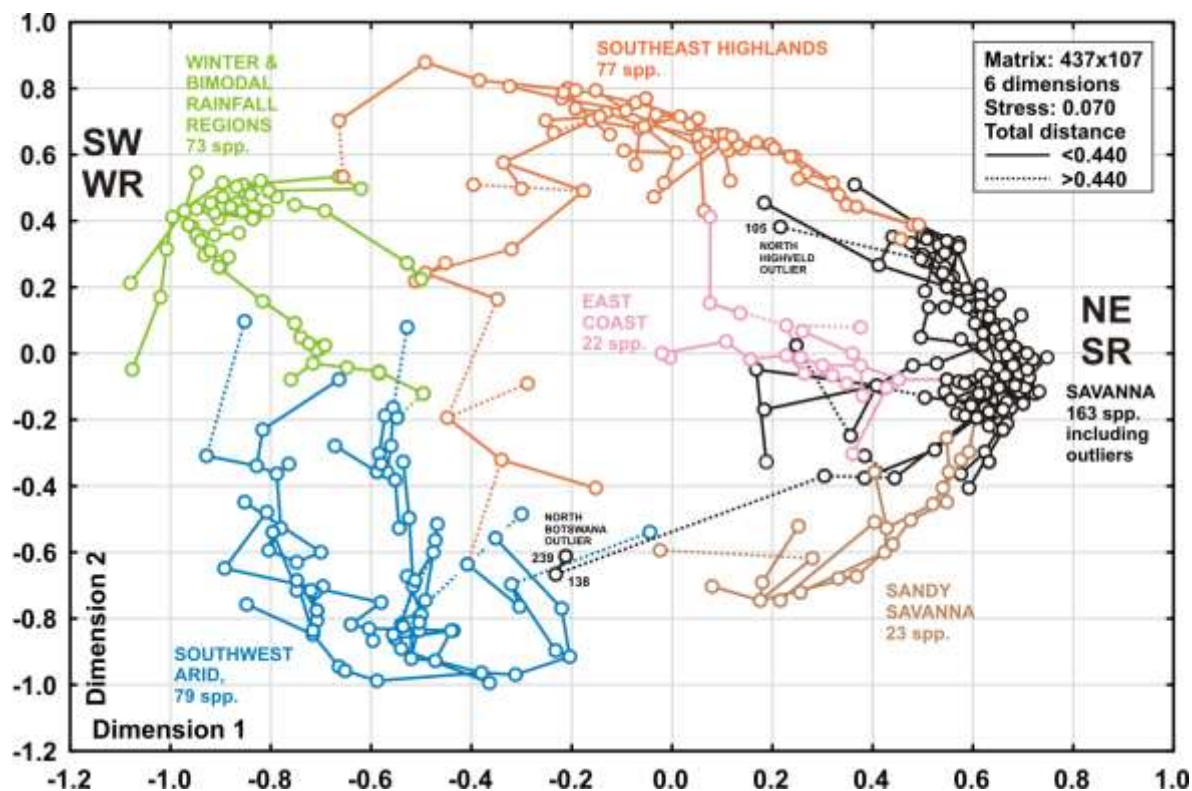


Figure 1. NMDS ordination biplot with minimum spanning tree indicating similarities between distribution patterns of 437 dung beetle species recorded in southern Africa that are subdivided into six regional clusters (SW WR = southwest, winter rainfall; NE SR = northeast, summer rainfall).

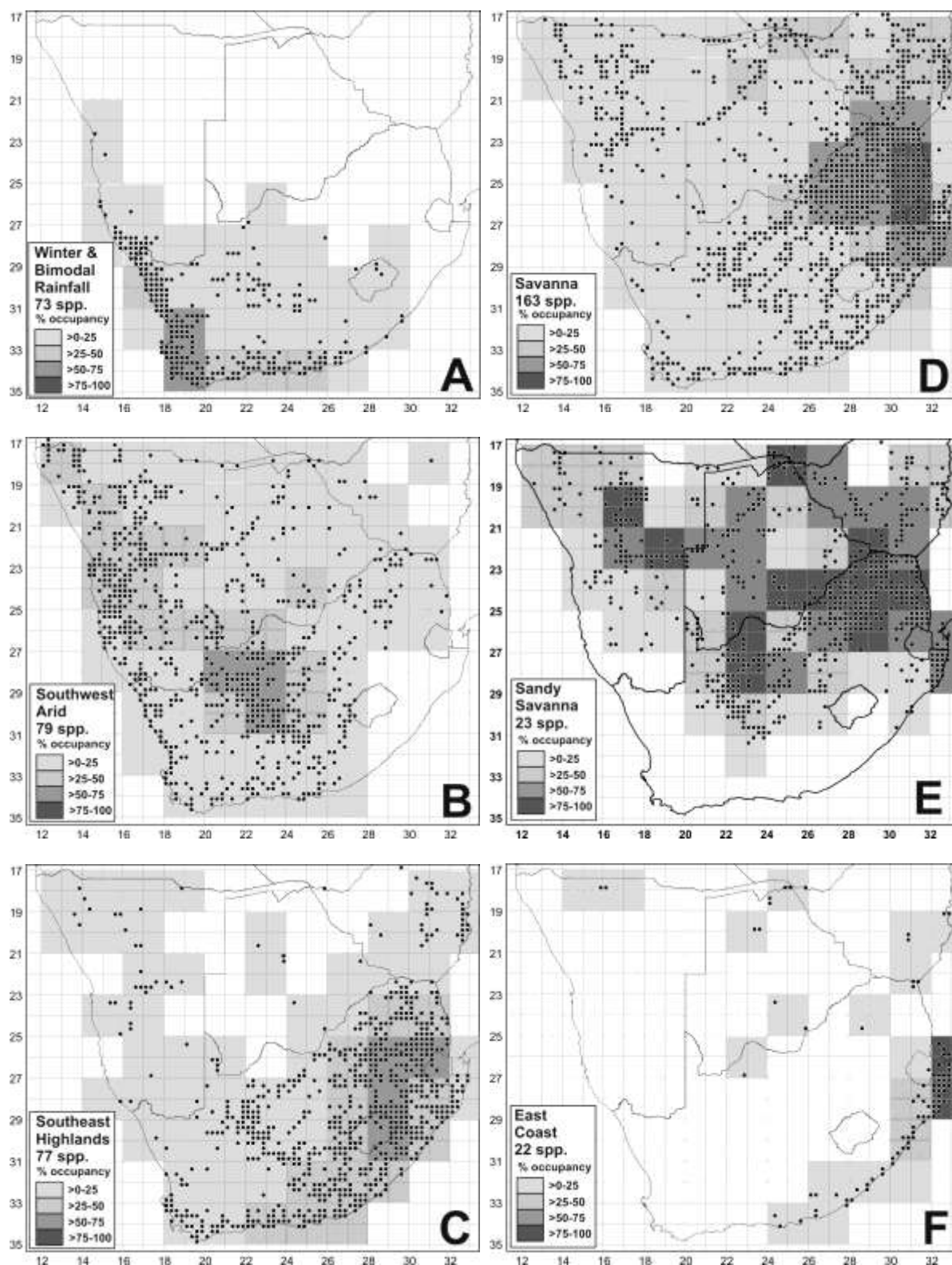


Figure 2. Range and distribution centres of dung beetle species in six regions defined for southern Africa (see Fig. 1).

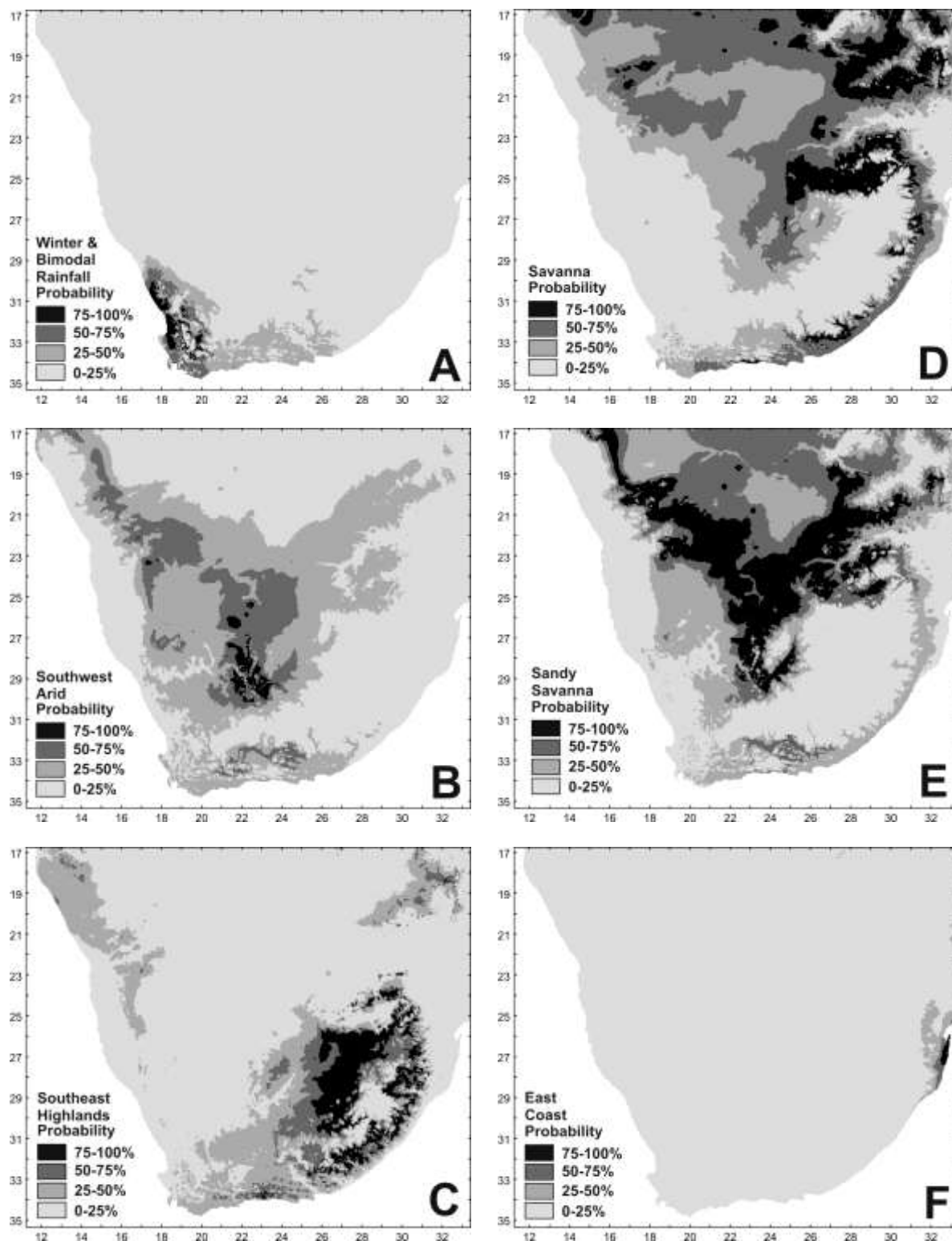


Figure 3. Probability of occurrence across southern Africa for groups of dung beetle species representative of six regional distribution centres (see Fig. 2).

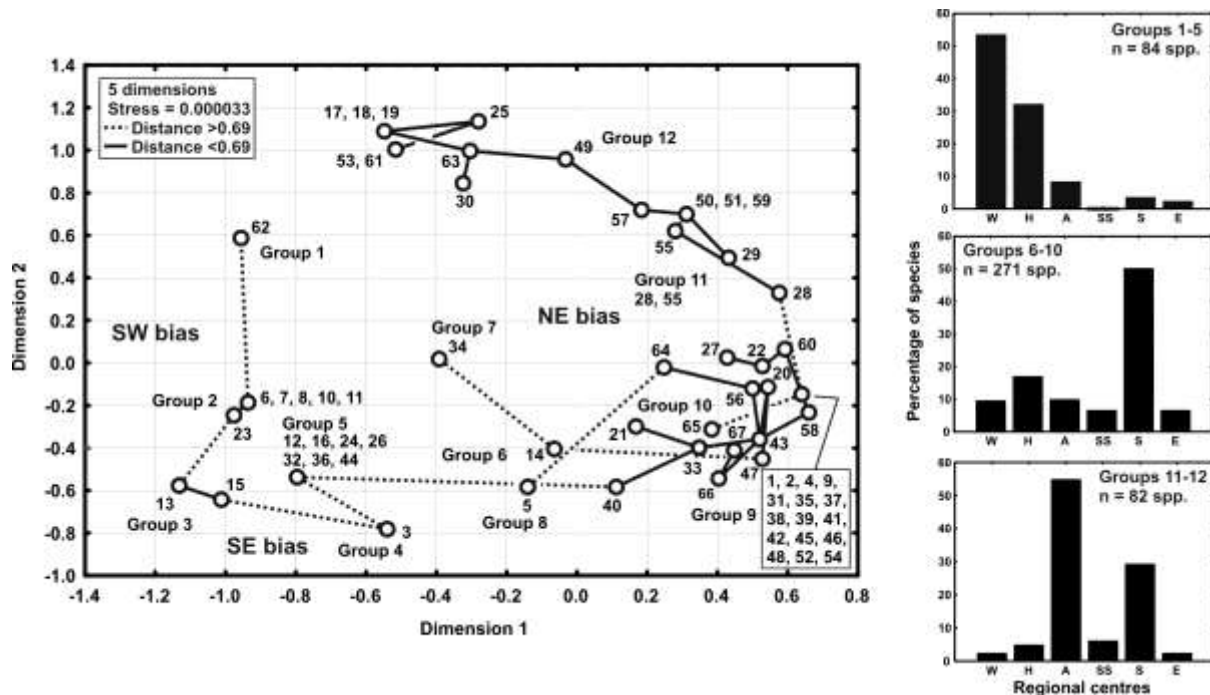


Figure 4. NMDS ordination biplot with minimum spanning tree indicating similarities between distribution patterns of 67 dung beetle genera recorded in southern Africa (see Supplementary Table S2 for key). For three generic groupings (1-5, 6-10, 11-12), bar diagrams indicate distribution of species between six regional centres (W = winter & bimodal rainfall, H = southeast highlands, A = southwest arid, S = savanna, SS = sandy savanna, E = east coast).

Subregional biogeographical patterns

A total of 27 subregional clusters were defined within four of the six regions (Fig. S2; Table S3) although only 21 were represented by >3 species (Fig. 5).

Six subregional clusters were defined from NMDS ordination of distributional data for 73 species centred on the winter and bimodal rainfall region (Figs 5A1, 5A2). From arid northwest to moister southeast, five subregional distribution patterns were centred on (Figs S3A-S3E): Namaqualand (S3A); west coast (S3B); southwest Cape (S3C); south Cape (S3D) and southeast Cape (not mapped). The remaining cluster was widespread in the winter and bimodal rainfall region and adjoining Nama Karoo (S3E).

Seven subregional clusters were defined from NMDS ordination of distributional data for 79 species centred on the southwest arid region (Fig. 5B). Six distribution patterns comprising >3 species were centred on (Figs S4A-S4F): Namib Desert (S4A); adjoining arid savanna (S4B); moister savanna of the north Namibian plateau (S5C); southwest Kalahari with marginal occurrences westward to the preNamib and/or west coast of South Africa, or, eastwards into savanna outliers (S4D); southwest arid from southwest Angola, through Namibia to central South Africa with marginal occurrences in the winter and bimodal rainfall region or savanna (S4E); Upper Karoo in south central South Africa with marginal occurrence on the southwest escarpment of Namibia (S4F).

Five subregional clusters were defined from NMDS ordination of distributional data for 77 species centred on the southeast highlands (Figs 5C1, 5C2). Three distribution patterns comprising >3 species were centred on (Figs S5A-S5C): west central Highveld and east Upper Karoo with marginal occurrence on the Highveld and south Cape (S5A); Highveld and east coast with marginal occurrence in the south Cape, east Zimbabwe highlands and north Namibian plateau (S5B); east scarp with marginal occurrence in the south Cape and east coast (S5C).

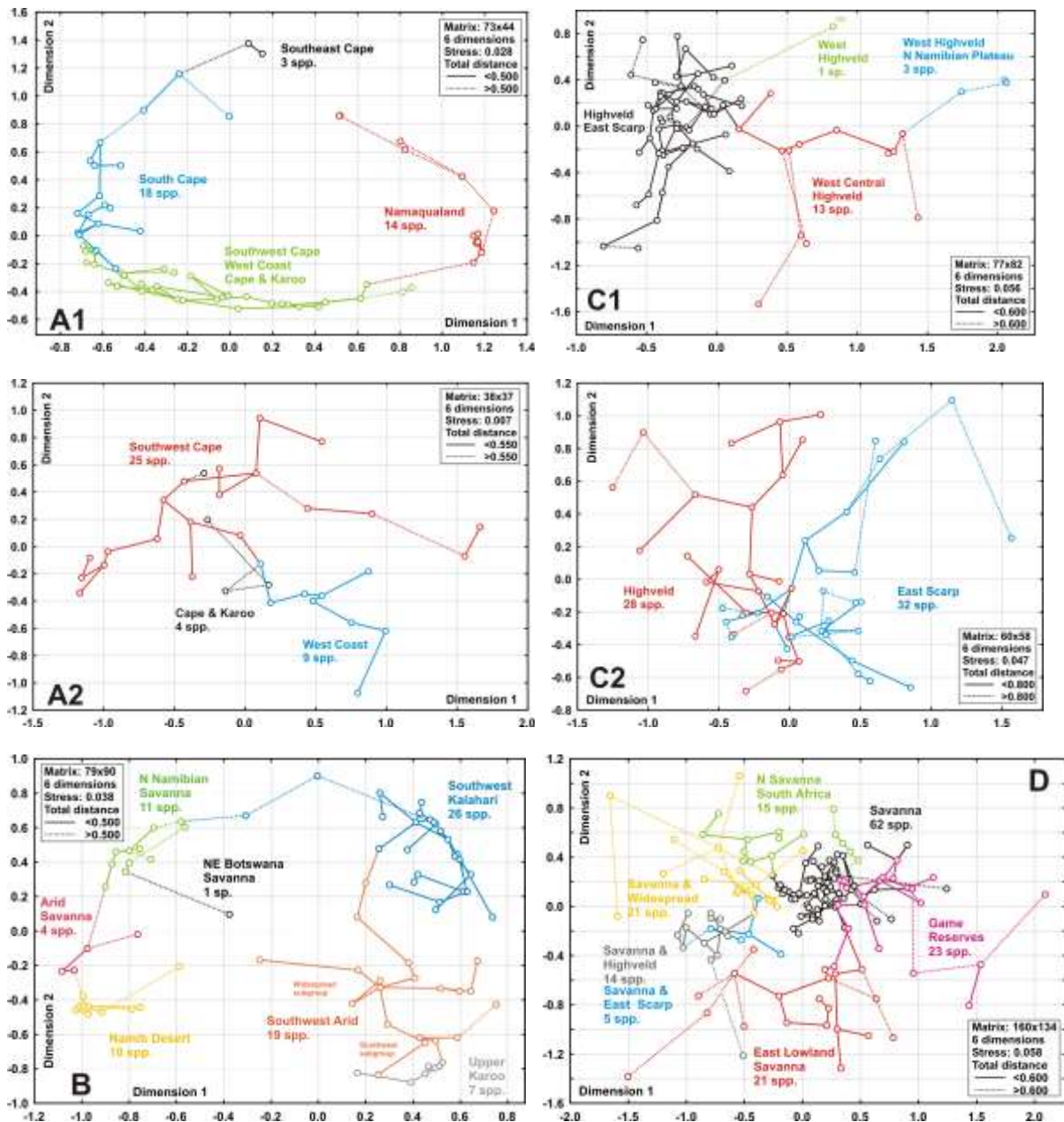


Figure 5. NMDS ordination biplots with minimum spanning trees indicating similarities between distribution patterns of dung beetles within four regions defined in Fig. 1: A1, A2. Winter & bimodal rainfall region (five subregions); B. Southwest arid region (seven subregions); C1, C2. Southeast highland region (five subregions), F. Savanna (seven subregions plus two more shown in Fig. 1) (see Supplementary Figure S2 and Table S3 for keys).

Nine subregional clusters were defined from NMDS ordination of distributional data for 163 species centred on the savanna region (Figs 1, 5D). Seven overlapping distribution patterns comprising >3 species were centred on (Figs S6A-S6F): north Highveld, north South Africa and Zimbabwe with widespread representation across the entire subcontinent, particularly the north Namibian plateau and south Cape (S6A); north South Africa and Zimbabwe with representation across all other savanna regions including the north Namibian plateau and Kalahari (S6B); uplands of north South Africa (S6C); uplands and east coast of South Africa plus east Zimbabwe uplands with marginal occurrence in the south Cape (S6D); lower east scarp of South Africa (S6E);

east lowlands of South Africa with marginal occurrence on the east coast and south Cape (S6F); game reserves in north Botswana, northwest Zimbabwe and northeast South Africa (Fig. S7A).

Environmental correlates

Spearman r values indicate strong correlations between environmental variables and ordinal values for the six dimensions extracted by NMDS analysis of distribution data for 437 dung beetle species (Table 1). Strongest correlations were shown along Dimensions 1, 2 and 3. Along Dimensions 1 and 2, annual rain, annual temperature and rainfall seasonality were significant influences with that of altitude not significant. Altitude was most influential along Dimension 3 with weaker significant influences of the three climatic variables. There were significant declines in temperature, rainfall and proportion of summer rain (Table 1, Fig. S8) from positive to negative values along Dimension 1 (Fig. 1), which reflect a gradient from northeast summer rainfall to southwest winter rainfall regions. However, from negative to positive values along Dimension 2, there was a significant increase in rainfall but declines in proportion of summer rain and temperature, which reflect a progression from hot, dry to cooler, often moister regions.

Table 1 Spearman rank order correlations between four environmental variables and ordinal values for six NMDS dimensions derived from analysis of spatial distribution of 437 species of dung beetles (Spearman r values >0.4 in bold; $*P<0.05$).

Dimension	Spearman r values			
	Annual temp.	Annual rain	Altitude	summer rain % [^]
Dimension 1	0.616*	0.643*	0.035	0.686*
Dimension 2	-0.589*	0.436*	-0.013	-0.474*
Dimension 3	-0.366*	0.143*	0.853*	0.154*
Dimension 4	-0.019	0.206*	-0.098*	-0.150*
Dimension 5	0.132*	0.015	-0.223*	-0.366*
Dimension 6	0.034	-0.031	-0.020	-0.221*

[^]Seasonality of rainfall: % from November to March (inclusive)

Most environmental attributes varied significantly between species groups showing different regional and subregional centres of distribution (Tables 2, 3), reflecting the disposition of these attributes across the subcontinent (Figs S1A-S1E). Groups centred to the southwest and southeast were subject to lower annual temperatures (southeast highland, winter and bimodal rainfall regions, plus southwest subregions of the southwest arid region: Upper Karoo, Namib Desert, arid savanna) (14.7-17.2° C). Those centred to the northwest were subject to higher annual temperatures (savanna, sandy savanna, east coast and northwest subregions of the southwest arid region: southwest arid, Kalahari, north Namibian savanna) (18.2-22.2° C). Groups centred to the southwest regions (winter and bimodal rainfall, southwest arid) were characterized by lower annual rainfall (63-411 mm) and those to the northeast (savanna, sandy savanna, east coast) and southeast (southeast highlands) by higher rainfall (492-817 mm). Proportion of summer rainfall was low in the winter rainfall region (30%) and its western subregions (14-28%; Namaqualand, west coast, southwest Cape) although it was subject to more summer rainfall influence along the moister south coast subregion of South Africa (47%). Across the remaining regions and subregions, there was a much greater bias to summer rainfall (63-87%). Altitude was unevenly distributed between regions and subregions. Although half of the subregions were centred at 800-1100 m, there were also lowland (east coast region, savanna game reserves and east lowland savanna subregions) to moderate

altitude (winter and bimodal rainfall region) (88-575 m) and highland centred areas (southeast highlands region, north Namibian savanna subregion) (1256-1423 m).

Table 2 Environmental data associated with regional species groups defined from NMDS ordination of distribution data for 437 species of dung beetles with results for Kruskal-Wallis ANOVA tests ($***P<0.001$) and multiple comparisons of mean ranks ($P<0.05$).

Regional centre (numbers of species)	Mean \pm S.D.^			
	Annual temp. ($^{\circ}$ C) (max.+min./2)	Annual rainfall (mm)	Altitude (m)	Proportion of summer rain (%) (Nov. to March)
Winter & Bimodal Rainfall (73 spp.)	16.8 \pm 1.0 ^a	282 \pm 149 ^a	336 \pm 252 ^a	30 \pm 16 ^a
Southwest Arid (79 spp.)	18.3 \pm 1.5 ^b	257 \pm 114 ^a	1063 \pm 215 ^c	73 \pm 10 ^b
Southeast Highlands (77 spp.)	15.5 \pm 1.9 ^a	702 \pm 156 ^{cd}	1331 \pm 338 ^d	70 \pm 4 ^b
Savanna (163 spp.)	20.1 \pm 1.5 ^c	666 \pm 95 ^c	806 \pm 281 ^b	77 \pm 4 ^c
Sandy Savanna (23 spp.)	20.2 \pm 0.7 ^c	502 \pm 80 ^b	973 \pm 126 ^{bc}	79 \pm 3 ^c
East Coast (22 spp.)	21.5 \pm 1.1 ^c	817 \pm 114 ^d	108 \pm 129 ^a	65 \pm 5 ^{ab}
H (5, N=437)	289.9 ^{***}	307.7 ^{***}	270.5 ^{***}	272.5 ^{***}

^Means of average values for each species across 5x5 km² map polygons (see methods).

In each column, values followed by a different letter differed significantly.

Table 3 Environmental data associated with principal subregional groups of dung beetles (>3 spp.) defined from NMDS ordination of distribution data with results for Kruskal-Wallis ANOVA tests (*** $P<0.001$) and multiple comparisons of mean ranks ($P<0.05$).

REGION Subregion (numbers of species)	Mean \pm S.D.^			
	Annual temp. ($^{\circ}$ C) (max.+min./2)	Annual rainfall (mm)	Altitude (m)	Proportion of summer rain (%) (Nov. to March)
WINTER & BIMODAL RAINFALL				
Namaqualand (14 spp.)	17.1 \pm 1.0	96 \pm 35 ^a	432 \pm 244 ^{bc}	28 \pm 18 ^{ac}
West Coast (9 spp.)	17.2 \pm 0.2	199 \pm 23 ^{ab}	140 \pm 46 ^a	14 \pm 4 ^a
Southwest Cape (25 spp.)	16.7 \pm 1.0	284 \pm 90 ^b	228 \pm 173 ^{ab}	21 \pm 8 ^{ac}
South Cape (18 spp.)	16.2 \pm 1.2	411 \pm 63 ^c	465 \pm 320 ^c	47 \pm 6 ^b
Cape & Karoo (4 spp.)	16.7 \pm 0.6	267 \pm 38 ^{abc}	575 \pm 65 ^c	36 \pm 6 ^{bc}
H (4, N=70)	8.15	52.15***	22.74***	42.46***
SOUTHWEST ARID				
Namib Desert (10 spp.)	15.7 \pm 0.8 ^a	63 \pm 21 ^a	783 \pm 306 ^a	64 \pm 14 ^{ab}
Arid Savanna (4 spp.)	16.8 \pm 0.8 ^{ab}	162 \pm 65 ^{ab}	943 \pm 391 ^{ab}	85 \pm 1 ^{cd}
North Namibian Savanna (11 spp.)	19.3 \pm 0.9 ^{cd}	407 \pm 97 ^c	1354 \pm 110 ^c	87 \pm 1 ^d
Southwest Kalahari (26 spp.)	19.4 \pm 0.5 ^d	299 \pm 48 ^{bc}	1065 \pm 80 ^{ab}	73 \pm 6 ^{bc}
Southwest Arid (20 spp.)	18.4 \pm 0.6 ^{bc}	228 \pm 44 ^a	1029 \pm 61 ^{ab}	69 \pm 4 ^{ab}
Upper Karoo (7 spp.)	16.7 \pm 0.8 ^{ab}	243 \pm 46 ^{abc}	1167 \pm 101 ^{bc}	63 \pm 2 ^a
H (5, N=78)	56.67***	55.01***	39.93***	49.18***
SOUTHEAST HIGHLANDS				
West Central Highveld (13 spp.)	15.3 \pm 1.3 ^{ab}	492 \pm 68 ^a	1295 \pm 283	65 \pm 4 ^a
Highveld (28 spp.)	16.4 \pm 0.9 ^b	736 \pm 68 ^b	1256 \pm 236	71 \pm 4 ^b
East Scarp (32 spp.)	14.7 \pm 2.4 ^a	795 \pm 112 ^b	1423 \pm 429	70 \pm 4 ^b
H (2, N=73)	14.27***	34.57***	2.02	17.57***
SAVANNA				
Savanna & Widespread (21 spp.)	18.7 \pm 0.6 ^a	625 \pm 99 ^a	1060 \pm 130 ^c	76 \pm 2 ^{ab}
Savanna (62 spp.)	20.3 \pm 0.9 ^b	646 \pm 63 ^a	814 \pm 185 ^b	79 \pm 3 ^{cd}
North RSA Savanna (15 spp.)	19.2 \pm 0.9 ^a	597 \pm 72 ^a	1082 \pm 135 ^c	79 \pm 2 ^{bcd}
Savanna & Highveld (14 spp.)	18.2 \pm 0.7 ^a	776 \pm 57 ^b	1010 \pm 160 ^{bc}	74 \pm 2 ^a
East Lowland Savanna (20 spp.)	20.6 \pm 1.4 ^b	785 \pm 89 ^b	410 \pm 210 ^a	70 \pm 4 ^a
Savanna & East Scarp (5 spp.)	18.2 \pm 1.0 ^a	804 \pm 65 ^b	1005 \pm 209 ^{bc}	75 \pm 2 ^{abc}
Game Reserves (23 spp.)	22.2 \pm 0.6 ^c	619 \pm 59 ^a	525 \pm 145 ^a	81 \pm 3 ^d
H (6, N=160)	104.99***	73.92***	105.37***	86.92***

^Means of average values for each species across 5x5 km² map polygons (see methods).

In each column within each region, values for subregions followed by a different letter differed significantly.

Patterns of small range size and endemism

A total of 160 out of 532 species (30%) showed small known ranges that were <20,000 km² (Table S3). These species were unevenly distributed between the nine tribes of dung beetles recorded in the subcontinent with four tribes accounting for the majority (140 spp.), one monophyletic (Scarabaeini) and three polyphyletic (Ateuchini, Deltochilini, Coprini - but see discussion of recent partial revision to tribal classification). Ranges of these species were centred around the southern African coastline and bordering mountain escarpments (Fig. 6) and coincided, especially, with parts of the winter and bimodal rainfall, southwest arid, southeast highlands and east coast regions (Figs 2; S3-S5). The first three of these regions are largely restricted to southern Africa and encompassed most of the generic and species endemism recorded in South Africa, Namibia and/or Botswana (Table 4).

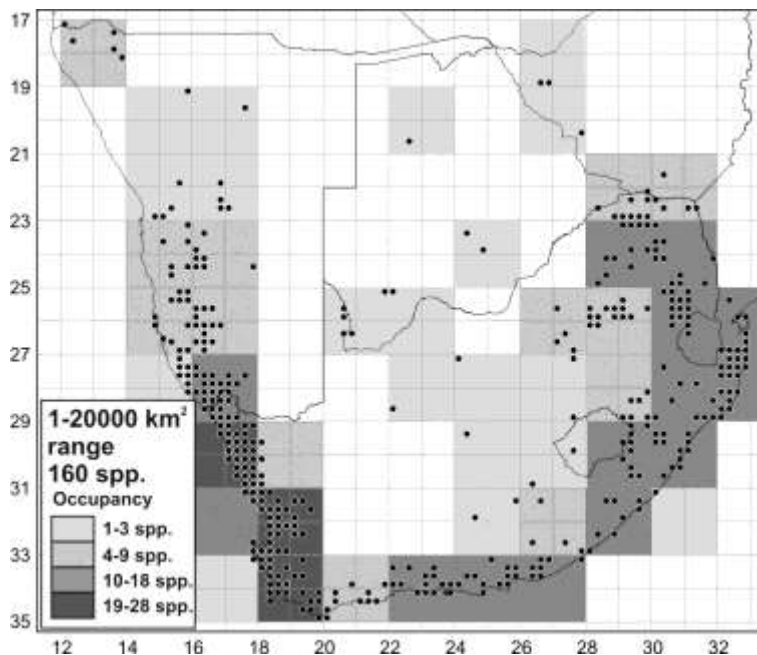


Figure 6. Combined range and distribution centres of 160 dung beetle species each showing extents of occurrence (EOO) of <20,000 km² in South Africa, Botswana and Namibia.

Table 4 Endemic dung beetle taxa within South Africa, Botswana and/or Namibia (includes Lesotho and eSwatini) according to known distributions reported by Davis et al. (In press).

Defined regional centre	N genera	N species	Endemic genera (%)	Endemic species (%)
Winter & Bimodal Rainfall	20	73	45.0	100.0
Southeast Highlands	28	77	21.4	89.6
Southwest Arid	25	79	16.0	60.8
Savanna	47	163	4.3	20.9
Sandy Savanna	14	23	0.0	4.4
East Coast	14	22	7.1	18.2

Discussion

Subcontinental, regional and subregional patterns

The present analysis of dung beetle distribution in southern Africa is considered to improve upon a previous analysis (Davis 1997) as it is based on a much more comprehensive data set, which yields an expanded and somewhat more hierarchical division into regional and subregional centres. Five of the six defined regional centres coincide with major climatic and vegetation regions across the southern African subcontinent (Walter & Lieth 1964; Olson et al. 2001; Mucina & Rutherford 2006) whereas the sandy savanna was additionally distinguished by edaphic criteria. The strong parallel in distribution patterns between dung beetles and vegetation regions is driven by opposing southwest and northeast climatic systems that produce winter rainfall to the southwest, aridity from a cold marine upwelling to the west, and summer rainfall to the northeast (Dieppois et al. 2016). Distribution of taxa centred on the southwest region (winter and bimodal rainfall) and west to southwest subregions (Namib Desert, arid savanna, Upper Karoo) were largely restricted in extent whereas those of most northeast regions and subregions showed wide overlap into the southwest regions with many, mostly savanna species, showing even wider ranges extending as far north as East Africa (Davis et al. In press). Although regional to subregional differences in rainfall, temperature, rainfall seasonality and altitude were strong correlates of geographical patterns in species distribution, they were also influenced by edaphic variation, vegetation cover and availability of preferred dung types. However, these ecological variables were more difficult to define due to the degree of soil variation (FAO 2012), vegetation disturbance (RSA: Fairbanks et al. 2000) and fragmentation of ranges for large indigenous mammals across much of Africa (Riggio et al. 2018). Nevertheless, from modelling of present regional centres, it may be predicted that any increase in temperatures from future climatic change might favour range expansion of northeast-centred dung beetle species at the expense of cooler-adapted southwest-centred taxa with increased abundance and dung removal to the southwest under warmer climate more influenced by summer rainfall.

Regional and subregional patterns

The six subregions defined for the cool winter and bimodal rainfall region result, especially, from beetle responses to rainfall, seasonality, edaphic character and vegetation. Five of the subregions occurred across a rainfall gradient southwards from arid Namaqualand along the west coast to the southwest Cape and eastwards along the moister south Cape coast. Furthermore, rainfall seasonality was biased to winter in the arid west (April to August: ~66%) becoming even in the west of the south coast (November to March: 45%) but biased towards summer in the east (67%) with poorly-defined bimodality during spring and autumn. Field records suggest that at least 46 out of 73 species (63%) show a bias to coarser-grained soils with at least 26 associated with deep coastal sands (Davis et al. In press) that are extensive along the west coast but limited in area along the south coast where finer-grained soils also occur (FAO 2012). Thus, the many coastal specialists help define the three western subregions with relatively few species centred solely on the finer-grained soils of bordering hills and mountains. As shrubland plant assemblages of the Succulent Karoo, Fynbos and Renosterveld Biomes, plus south coast forest patches, dominate in the winter and bimodal rainfall region (Mucina & Rutherford 2006, Potts et al. 2015), vegetation cover was an important influence on endemic dung beetles (Davis 1993; Davis et al. In press). Of 33 winter and bimodal rainfall species of the southwest Cape, 55% (18) were significantly more abundant in natural, shrubland, a further four species were vegetation generalists and 30% (10) were more abundant in grassland pastures created by clearance of the natural shrubs (Davis 1993). Of 12 species from biogeographical groups centred to the northeast in the summer rainfall region, 67% (8 spp.) were significantly more abundant in pasture, three species were vegetation generalists and only one was found primarily in shrubland (Davis 1993). Furthermore these summer rainfall species (Regions: Highveld: 4 spp.; southwest arid:

5 spp.; savanna: 3 spp.) were primarily active in the warm, dry summer of the southwest Cape whereas the 33 endemic species were primarily recorded in the cool, moist spring and/or autumn.

The southwest arid region is characterized by rainfall peaks from January to April in late summer. These peaks vary from 58-85% of annual precipitation across six main subregions. The subregions result, especially, from beetle responses to rainfall and temperature gradients, plus edaphic characteristics, with vegetation effects uncertain across a gradient from desert, grassland, shrubland to open woodland plant assemblages (Olson et al. 2001; Mucina & Rutherford 2006). Across the deep sands of the Botswana Kalahari from the mesic northeast (Chobe National Park) to the arid southwest (Kgalagadi Transfrontier Park), 88% (23) of the Kalahari species showed an extreme southwesterly bias (Tshikae et al. 2013a). In the case of 21 species, >95% of their abundance occurred in the southwest, thus, supporting the arid southwest centre of distribution defined for the subregion. The three southwestern subregions are cooler as they either border the Namibian coast that is subject to mists generated from the cool Benguela Current (Cermak 2012) (arid: Namib Desert, arid savanna), or, they occurred on southern uplands (moister: Upper Karoo). The three northwestern subregions of the interior were much warmer despite differences in mean altitude (moister: north Namibian savanna, southwest arid, Kalahari). Dominant soil types varied between subregions from coarser-grained, deep sands (Namib, Kalahari) or finer-grained, sandy loams to clay loams (southwest arid, Upper Karoo, north Namibian savanna) (FAO 2012) with many rocky areas along the Namibian escarpment that support an endemic group of hyrax-associated taxa (arid savanna) (Deschodt & Davis 2018). Namib Desert species are centred on extensive dune fields (70% = 7 spp.) or gravel plains. Most Kalahari species are sand specialists (23 = 88%) (Davis et al. In press) with their wider distribution dictated by occurrence of sands on the west coast or in eastern savanna outliers. In the Northern Cape (South Africa), Kalahari soils were significantly more sandy than in the adjoining areas of the southwest arid or Upper Karoo subregions where Kalahari species were uncommon (Davis et al. 2016). By contrast, southwest arid species were proportionally more common at the edge of the southwest Kalahari, perhaps because their soil associations are less well defined. However, a few southwest arid species (*Scarabaeolus fritschi*, *S. pabulator*) that are recorded primarily from sands of dry saline pans (Davis et al. 2016) were uncommon in the Kalahari. Therefore, a mixture of factors may play a part in separating these two subregions, including climate, soil type and species interactions.

The cool southeast highlands were divisible into three, major, highly overlapping subregions receiving most rainfall during summer (November to March: 65-71%). Subregional distribution centres occurred in sequence from the dryer west central to moister central and cooler, moister, east escarpment of South Africa. Some members of all three main subregions were also represented along the warmer east coast and cooler south coast diminishing in representation to the west in the winter rainfall region. Few of these species also occurred on other warmer highlands in east Zimbabwe or the north Namibian plateau. Field records show that most species of the Highveld and east scarp subregions occur on finer-grained soils (Davis et al. In press), although these dominate across the region (FAO 2012). They also show that most occur in grassland although this vegetation type also dominates across the region (Mucina & Rutherford 2006). By contrast, a few are range-restricted specialists in upland forest patches along the east escarpment (Davis et al. In press) (i.e. nine out of 77 spp. with others excluded from the analysis).

The warm savanna region of northeast southern Africa was divisible into seven main subregions centred on the moister east savanna that is dominated by open or closed shrub / woodlands receiving most rainfall during summer (70-81%). Although there was high spatial overlap between species groups defined from around the MST tree periphery, there were significantly different between-group trends in temperature/altitude and rainfall. Two subgroups within the north RSA savanna group represent species centred on the Central Bushveld of Mucina & Rutherford (2006) or the Soutpansberg area of South Africa. Of the species included in the game reserve group, 87% (20) were primarily recorded from the dung of monogastric herbivores in field

collections (Davis et al. In press). However, quantitative data for 11 of these species (Tshikae et al. 2013b; Davis et al. 2014) either show a bias to monogastric herbivore dung (5 spp.) or to omnivore dung (pig; 6 spp.). Nevertheless, as a group, they showed disjunct distributions centred mainly on national parks (Chobe in Botswana, Hwange in Zimbabwe, Kruger in South Africa) or game reserves (uMkhuze and iMfolozi-Hluhluwe, South Africa). Despite the northeast centres of distribution, ranges of many savanna species extended into dryer (western savanna) and/or cooler climates (southeast highlands), some with differing rainfall seasonality (south to southwest coast). However, the summer activity period of the species is largely retained throughout their ranges, even in the winter and bimodal rainfall regions of the south and southwest Cape where dry summers result in low abundance. This excludes *Onitis caffer* Boheman that shows autumn / winter activity throughout its range.

Although the sandy savanna region is climatically similar to the savanna subregion (Table 2), its widespread, northwest to northeast distribution centre differs to the easterly bias shown by all seven savanna subregions. The difference results from domination by species (87% = 20 spp.) that are mostly centred on sandy soils (7 spp.) and deep sands (13 spp.) found in the Kalahari, east savanna and east coast (Doube 1991; Davis 1996a; Davis et al. 2016, In press). A total of 83% (19) of the species were recorded along an environmental gradient across the Botswana Kalahari from the mesic northeast to arid southwest (Tshikae et al. 2013a). Two thirds of these 19 species (58% = 11) showed a strong bias (>88% of abundance) to the mesic northeast.

In South Africa, most species of the east coast region are centred on the warm, moist, Indian Ocean Coastal Belt biome of Mucina & Rutherford (2006). Although a few species are centred to the southeast in the Pondoland Centre of Endemism (*Gyronotus pumilus*, *Epirinus convexus*), most are, currently, known primarily from the Maputaland Centre of Endemism in northeast KwaZulu-Natal / southeast Mozambique where 94% (17 spp.) show a bias to deep coastal sands with 50% (9 spp.) in forest, 33% (6 spp.) on grassland of fossil lagoons and 17% (3 spp.) in open woodland (Doube et al. 1988; Doube 1991; Davis et al. 2002, 2013, In press; F. Escobar unpubl.). Although most of these species are currently regarded as east coast endemics, some with more northerly distributions (outside of the map panel) also occur up sandy river valleys, particularly the Zambezi, penetrating to sandy floodplains in north Botswana and north Namibia.

Taxonomy, biogeography and conservation

Dung beetle regions and subregions of the southwest are characterized by endemic species with quite different patterns of generic and tribal affiliation to those in the northeast (Table S2). However, higher classification of the subfamily Scarabaeinae is currently in disarray as three tribes (Ateuchini, Deltochilini (=Canthonini), Coprini) are clearly polyphyletic (Philips et al. 2004; Monaghan et al. 2007; Tarasov & Génier 2015; Tarasov & Dimitrov 2016) leading Davis et al. (2019) and Daniel et al. (2019) to recently reassign some southern African Deltochilini to four new tribes of which three are endemic to Namibia and/or South Africa. In southern Africa, membership of the three strongly polyphyletic tribes comprises separate groups of generic lineages for Deltochilini (~7 - includes two recently reassigned to new tribes), Ateuchini (2) and Coprini (~4). Together with the Scarabaeini, these three tribes show a unimodal trend to small ranges or a bimodal pattern of bias to both small and larger ranges (Table S1) with some genera and/or species showing a distinct southwest or southeast highland centre of distribution. The five remaining tribes show a unimodal trend to larger ranges that reflects their northeast bias to spatially, more extensive, summer rainfall climates. The patterns suggest different histories of origin and biogeographical centring that would each require different conservation strategies.

Along with the disarray in classification, the historical origin and relative age of the different major taxa are controversial (Mlambo et al. 2015; Ahrens et al. 2014; Gunter et al. 2016; Davis et al. 2017). This complicates a synthesis of biogeographical history for southern Africa. Based on known patterns, it might be hypothesized that eco-climatic history since the late Miocene has driven evolution of endemic southwest dung

beetle genera with only limited addition of genera that have many tropical relatives. Although further molecular systematics study would be required to support or disprove such hypothesized directionality, it is noteworthy that southwest endemics comprise many flightless taxa characteristic of forest litter, fynbos shrubs, desert (Davis et al. In press) and hyrax middens along the arid west escarpment (Deschodt & Davis 2018). Most flightless taxa are currently classified in the Scarabaeini or the three polyphyletic tribes with some occurring on lineages with the oldest origins (Mlambo et al. 2015).

Endemism has presumably been driven by eco-climatic evolution since the late Miocene. In the southwest, tropical coastal forest has been replaced by cool winter rainfall shrubs and forest patches with aridity developing to the north (Diekmann et al. 2003; Dupont et al. 2011; Hoetzel et al. 2015; Sciscio et al. 2016). This is consistent with the evolution of *Pachysoma* (tribe Scarabaeini) along the arid west coast that has been dated to the Plio/Pleistocene (Sole et al. 2005). In the southeast, uplift has, presumably, driven development of cool grassland and upland forest (Neumann & Bamford 2015). There is limited incursion into the southwest by species in the tribes, Gymnopleurini, Sisyphini, Onitini, Onthophagini and Oniticellini, that are better represented to the northeast in the savanna. In these tribes, a few endemic species in the southwest are limited to only the Sisyphini, Onitini and Onthophagini. However, recent penetration into the southwest by various northeast centred species may have increased due to the clearance of natural shrubland and the creation of pastures (Davis et al. In press).

Current conservation challenges

Other than range restriction of the indigenous large-bodied mammal fauna (Olson et al 2001), there is limited environmental modification in Namibia and Botswana compared to South Africa where there is both advanced habitat fragmentation and mammal range restriction. Urbanization, resource exploitation and agro-ecosystem development modified 20% of the land surface by the beginning of the new millennium (Fairbanks et al. 2000) although this has occurred asymmetrically. Whereas the arid western half of South Africa is rated as least concern, vegetation regions along the south and east coasts, plus most of the moist northeast, are rated as vulnerable to endangered with Renosterveld, in particular, rated as critically endangered (Mucina & Rutherford 2006). Thus, many dung beetle species of the winter and bimodal region, east coast, east scarp and north South African savanna are centred on highly transformed areas. By definition, many of their characteristic species comprise southwest or east seaboard endemics showing small restricted ranges in fynbos, renosterveld, grassland, woodland or forest (140 out of 160 spp. with known ranges (EOO) <20 000 km²). These habitats of the coastline and bordering escarpments occupy only small areas of South Africa. By contrast, widespread species are mostly centred on larger inland regions where degradation is limited (southwest arid) or where the effects of habitat degradation, cultivation, improved pastures or tree plantations are, possibly, mitigated by larger ranges, i.e. west and central Highveld, but, particularly savanna, where many species have distributions extending northwards into lower latitudes.

Habitat fragmentation or modification remains an increasing threat to some dung beetles that are vegetation and/or food specialists with even soil type specificity important if it coincides with loss of preferred vegetation. Although soil, vegetation and dung type associations are discussed for each of 541 species of southern African dung beetles (Davis et al. In press), findings for many of these species are drawn from variation at regional scale, unpublished data or qualitative field observations. Standardized quantitative data comparing grassland, open woody vegetation and/or shaded habitat at local scale exist for only small subsets of the fauna of South Africa, primarily for the Savanna or Indian Ocean Coastal Belt biomes of northeast KwaZulu-Natal (Doube 1983, 1991; Davis et al. 2002), Savanna or Grassland biomes near Pretoria/Tshwane (Davis 1996a; Davis et al. 2005) and the Fynbos biome near Cape Town (Davis 1993). These studies suggest that species associated with partially to strongly shaded woody vegetation are negatively affected by its

removal, particularly forest, dense savanna woodland and winter rainfall shrubland specialists. Moderate to strong effects on many species also result from (1) degradation or modification of grassland vegetation by overgrazing that induces reduced cover with increased surface temperature and hardening of the soil surface, (2) improved pastures of grasses with differing cover characteristics or (3) development of tree plantations (Davis et al. 1999, 2004; Jankielsohn & Scholtz 2001). Some of these vegetation types coincide with particular soil types to which some species are also specialized (Davis 1993, 1996a). Effects of past changes in occurrence of indigenous mammal fauna may be suggested by (1) clear clumping of a species group on savanna areas where there are large game reserves containing elephants and (2) by the diversity of *Scarabaeus* species in one Highveld reserve (Davis et al. 2005) that conserves many species of antelope that are now lost from most of the Highveld. These patterns suggest a current need to conserve indigenous Highveld grassland as well as all wooded areas, particularly forests, fynbos and, most urgently, the critically endangered Renosterveld, which harbours two extremely rare flightless species of *Copris* (Davis et al. In press). Preservation of indigenous mammal fauna would also be important, particularly large monogastric herbivores and Highveld antelope. Conservation strategies for individual species are outlined by Davis et al. (In press).

Potential future conservation challenges

If greenhouse gas emissions remain uncontrolled, it is predicted that, by 2070 (Rintoul et al. 2018), average global temperature will have increased by 3.5° C compared to the late 19th century (IPCC 2013). Nevertheless, limited climatic change is predicted for southern Africa, by 2100, compared to other world regions (Giorgi 2006). However, there is potential for radical change at the southern tip of Africa in the context of evolution of the regional eco-climatic system during the late Cenozoic. Although reversion to the tropical southern climate of the early Miocene (Dupont et al. 2011; Sciscio et al. 2016) currently seems remote, Steffen et al. (2018) have recently considered potential for development of a "hothouse earth". Such predictions are consistent with those for a 1.5° southwards latitudinal movement of the westerlies by 2100 (Swart & Fyfe 2012) and irreversible ice loss from some parts of Antarctica by 2070 (Rintoul et al. 2018). Thus, if change is unchecked, there is a potential for reduction or loss of the winter rainfall region following the southwards retreat of the Polar Front. Shift in the position of the southwest arid region or its ultimate loss would, presumably, be dependent on positional change, reduction or loss of the cold Benguela upwelling.

It is predicted that the biota of the cooler, southern biomes of South Africa face the greatest threats although these would be relatively minor up until ~2050 (Ziervogel et al. 2014). The Highveld grassland biome has been identified as particularly prone to change although other southern and eastern biomes would also be significantly influenced including the Nama Karoo, Indian Ocean Coastal Belt, Fynbos and Forest. Using predicted increases in CO₂, temperature and rainfall (IPCC 2007), modelling of vegetation changes within Africa predicts expansion of tree-dominated ecosystems to the southwest by 2100 (Scheiter & Higgins 2009), thus modifying the grassland biome, southwest Kalahari and northeast Nama Karoo that are currently dominated by grassland and/or shrubland. Assuming future increases of 2° C (see Erasmus et al. 2002) or 3.5° C (see Rintoul et al. 2018) in average global temperatures, a crude assessment of dung beetle data in Table 2 implies that temperatures in the cooler southwest would increase to parallel those currently experienced to the northeast. However, it should be noted that the standard deviations reported in Table 2 are based on those between mean values for each species in subregional groups. Much greater deviation around means for each species are reported by Davis et al. (In press) since individual records are often spread across a wide climatic range. Thus, many species may show greater climatic adaptability than that implied by Table 2.

Under scenarios of moderate climatic change, modelling techniques predict contractions of species range and/or species diversity in South Africa. Close on a third of the South African bird species studied by Coetzee et al. (2009) are predicted to lose climatically suitable space by 2070 to 2100 with range contraction

trending towards the east, south and escarpment regions. This translates to a potential 30-40% decrease in richness of fynbos and grassland bird species by 2085 (Huntley & Barnard 2012). Predictions based on a wider range of animals (Erasmus et al. 2002 - total 199 spp. - birds, mammals, reptiles and five orders of insects including dung beetles) suggest that a doubling of atmospheric CO₂ would induce an overall 2° C rise in temperatures with concomitant effects on rainfall patterns that would drive range expansions (17%) or range contractions (78%), primarily in an easterly direction across South Africa (41%) with fewer in a westerly direction. Under the considered scenario, few species showed no response (3%) or local extinction (2%). However, predicted changes in range indicate that the current reserve system would become less effective for protection of biota in the future, for instance, in the case of birds currently protected in the Kruger National Park (Coetzee et al. 2009).

Determination of current conservation strategies for dung beetles has been impacted by poor quality of distribution data (Koch et al. 2000), which complicates predictions for effects of future climatic change. Subsequent improvement of the database has permitted an improved analysis of distributional centres. However, at present, only a limited attempt has been made to model distributions useful for conservation strategies or determining effects of future change. Modelling is often somewhat simplistic and needs to be refined to identify the most important driving factors in order to predict putative changes in species ranges and community dynamics with more accuracy (McMahon et al. 2011). Dung beetle ranges are influenced not only by climatic factors (temperature, rainfall) but also by coincidence of predicted changes with suitable ecological conditions such as soil type, vegetation cover (shaded or unshaded) and availability of particular dung types. Furthermore, as initiation and duration of dung colonization activity by adults varies with diel and seasonal temperature cycles (Davis 1996b, 1996c), it is the temperature and rainfall data suitable for daily and seasonal activity by adults of each species that should be used for modelling although this should also be placed within the context of the diel and seasonal ranges shown by annual data.

Favourable conditions for dung beetle activity require coincidence of seasonal rainfall with suitable seasonal temperatures. Dung beetle seasonality differs between winter, late summer and mid summer rainfall regions (Davis 2002) although it has been studied only in the winter rainfall (Davis 1993) and mid-summer rainfall regions (Davis 1996c). In the mid summer rainfall region, abundance (Fig. 9) and species richness (Davis 2002) far exceeds that on the southwest coast, possibly, because warmer conditions during the seasonal activity peak favour larger populations and a species rich night-flying component that is limited to very few species in the endemic component of the southwest coast assemblage. Furthermore, under sunny conditions during these seasonal peaks, the morning peak in daily flight activity commences at approximately 24° C in the mid-summer rainfall region (Davis 1996b) and at about 20° C on the southwest coast (ALV Davis pers obs).

Modelling suggests that warmer climate in southern Africa would drive many species to track suitable cooler conditions at higher altitude or more southerly latitudes (Coetzee et al. 2009). Species most at risk of extinction might be those with small ranges centred at extremes of high altitude or southwest climate. Expansion of tree-dominated systems under warmer climate (Scheiter & Higgins 2009) implies possible replacement of grassland by savanna dung beetle species across parts of the Highveld. Upward shift and contraction of grassland habitat might be expected to be detrimental to endemic grassland species. Owing to its naturally-fragmented pattern, the Forest biome harbours many flightless endemic taxa belonging to putative ancient lineages. However, the capacity to track suitable climate across both altitude and latitude is much reduced in a human modified landscape (Eeley et al. 1999). In the southwest, seasonality of rainfall could shift from winter towards summer, which would be detrimental to the endemic fauna that is currently active primarily during the spring and autumn when rainfall coincides with suitable cool temperatures (Davis 1993). Such a trend might favour species centred in the summer rainfall region that currently show primarily dry summer activity in pastures created from clearance of indigenous shrubland. Within the southwest arid region, temperature increase

might drive southwards range expansion of sandy savanna elements and greater overlap with southwest Kalahari elements. Some potential range changes might fail to coincide with deep sands. Cool, west seaboard temperatures and low rainfall would likely increase with reduction or loss of the cool Benguela upwelling and might impact on ranges of west coast endemics, particularly in Namaqualand and the Namib Desert. As dung beetle assemblages comprise a competitive hierarchy (Hanski & Cambefort 1991), future climatic and ecological change could drive rearrangement of assemblage structure as has been indicated for past climatic changes (Chytrý et al. 2017). However, without precise measurements for input into models, it will be difficult to determine the exact nature of potential species losses or additions.

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Compliance with ethical standards

There is no conflict of interest. Under contractual conditions attached to JRS Biodiversity Foundation grant no. GNT60313 to CHS, the database created by the former Scarab Research Group has been made publicly available by upload onto the website of the Animal Demography Unit at the University of Cape Town <<http://vmus.adu.org.za/>>.

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