Soil type, vegetation cover, and temperature determinants of the diversity and structure of dung beetle assemblages in a South African open woodland and closed canopy mosaic

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Abstract Regional biogeographical patterns result from a complex combination across habitat, climate, and environmental variables. Biotic and abiotic variables strongly influence the diversity and spatial distribution patterns. However, very few studies analyse the close interaction and effect of environmental variables on diversity at fine spatiotemporal scales. In this study, we evaluated the influence of soil type, vegetation cover, and temperature on species diversity and functional structure of dung beetle assemblages. Dung beetle species were sampled using pitfall traps baited with cattle dung from sandy and clay soils in open woodland and closed canopy areas in Mkhuze Game Reserve, KwaZulu-Natal, South Africa. We performed a PERMANOVA, a PERMDISP, and an NMDS to analyse differences in species composition between soil and vegetation cover types. To test the effect of environmental variables on species richness and abundance, we performed a Generalized Least Squares model. Lastly, we searched for nodes using a bipartite analysis to evaluate network's potential modularity. We collected 1439 specimens comprising 27 species and 13 genera. Species composition differed between environmental variables. Soil type was the most important driver for changes in dung beetle species composition. Species richness and abundance were influenced by the interaction between soil type and vegetation cover. The combination of microenvironmental preferences potentially influenced the dung beetle assemblage diversity and functional structure. Combining all these preferences may act as a dilution mechanism of interspecific competition in saturated habitat conditions, reducing the number of species that potentially interact and generating a modular network structure of the assemblage.

Key words: competition dilution mechanisms, environmental variables, functional groups, micro-niches, Scarabaeinae.

INTRODUCTION

Interaction of effects of climate and habitat changes affect the global biogeographical patterns which influence the taxonomic composition, diversity, and abundance of several groups of insects (Wilson & Fox, 2021), including dung beetles. Historical distribution patterns of dung beetles result from a complex interaction across plate tectonics, vicariance, orogeny, dispersal and several climatic shifts (Davis *et al*. 2002; Daniel *et al*. 2020; 2021). However, at a regional or local scale, aspects such as habitat fragmentation, climate, or environmental variables tend to have a more critical effect (Davis 1993; Davis *et al*. 2008; 2014). In this context, several studies have shown that environmental variables such as vegetation cover, soil type, and temperature directly affect the structure and diversity of communities (Davis *et al*. 2008; Otavo *et al.* 2013; Davis *et al.* 2014; Davis & Scholtz 2020; Noriega *et al.* 2021). In the same way, these variables could influence and determine structural aspects such as composition and diel activity, generating functional groups with marked and specific rhythms throughout the day (Davis 1996a; Lobo *et al.* 2019) and finally affecting potential interactions and reducing competition between species.

Dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae) are strongly influenced by environmental changes and differences at broad and fine scales. This strong influence between abiotic and biotic conditions has regarded them as bioindicators (Halffter & Favila 1993; McGeoch *et al.* 2002; Spector 2006; Nichols *et al.* 2007; Otavo *et al.* 2013). Furthermore, this taxonomic group has a tremendous ecological relevance, not only for its prominent role in the decomposition process and nutrient cycling, but also for several additional ecosystem services related to dung and soil removal, aeration, soil permeability, parasite suppression and fly control, secondary seed dispersal, and potential reduction of greenhouse gas emissions (Andresen 2002; Bang *et al.* 2005; Nichols *et al.* 2008; Midgley & White 2016; Slade *et al.* 2016). Also, dung beetles are categorised into four main functional groups according to the type of food relocation and nesting pattern (Doube 1990): i) tunnellers (or paracoprids) make vertical tunnels under the dung pile; ii) rollers (or telecoprids) move a portion of dung horizontally, and after a certain distance they bury it; iii) dwellers (or endocoprids) do not relocate any portion of the dung pile either vertically or horizontally, they live inside it or at the dung-soil interface; iv) stealers (or kleptocoprids) parasitise the nests of other beetles, mainly tunnellers or rollers (Bornemissza 1976).

The diversity and spatial distribution patterns of dung beetles are strongly influenced by biotic variables such as mammal diversity (Davis & Scholtz 2001; Sands *et al.* 2021), vegetation cover (Cambefort 1982; Doube 1983; Davis & Scholtz 2020), and abiotic variables such as soil type (Nealis 1977; Davis 1996b; Doube 1983) and temperature (Davis 1996a; Lobo *et al.* 2019).

From a worldwide perspective, Africa is one of the most species rich continents for dung beetles with more than 2000 known species (Doube 1991). African regions can sometimes accommodate more than 100 species per locality (Doube 1987; 1991; Davis & Dewhurst 1993; Davis *et al*. 2014; 2016). This high regional diversity of dung beetles is a clear result of the interaction of macro and micro ecological variables that could generate a broad spectrum of habitats and environmental gradients closely associated with a high richness of vertebrates (Davis *et al*. 2012; 2014). However, large indigenous mammals have become extinct over vast regions of Africa, especially in Southern Africa where, they are restricted mainly to game reserves. Because of this pattern, dung beetles that have a specialised relationship with type of dung resource, have become rare in many regions and their distribution areas have been dramatically reduced (Davis & Scholtz 2020).

In this context, many dung beetle species use similar limited resources, which makes the resource availability a determining factor in the structure of dung beetle assemblages. The main result of this ecological pressure is resource partitioning in space and time, related to biotic and abiotic preferences associated with i) vegetation cover, ii) soil type, iii) diel activity, iv) dung type, and v) seasonal patterns (Doube 1991). The potential interaction between these preferences could act as an efficient dilution mechanism of interspecific competition in saturated habitat conditions, especially with ephemeral resources such as mammal dung (Hanski 1990), generating a modular structure in terms of the assemblage composition. Despite the vast knowledge of the ecology of this group (Halffter & Mathews 1966; Scholtz *et al*. 2009; Simmons & Ridsdill-Smith 2011), there are very few studies that analyse the effect of environmental variables and their interaction (*e.g*., soil type, vegetation cover, temperature) on diversity, structure (*i.e*., composition, richness, abundance, and functional groups), and daily activity of dung beetle assemblages at a fine scale (*i.e*., sampling resolution that allows to evaluate daily activity related to variations of temperature across different habitats). Here, we evaluate the influence of soil type (sand and clay), vegetation cover (open and closed), and temperature on species diversity and functional structure (composition, richness, abundance, and functional groups) of dung beetle assemblages in four habitats in South Africa. As a hypothesis, we predict that the combination of microenvironmental variables will strongly affect and significantly change dung beetle assemblage diversity and structure across different habitats. This study will help to identify species particularly associated with each of the combination of variables, which could help to generate specific conservation strategies for each one of them.

MATERIALS AND METHODS

Study area

Mkhuze (uMkhuze) Game Reserve comprises 400 km^2 in northern Zululand, KwaZulu-Natal, South Africa. The reserve has a diversity of natural habitats, including acacia savanna, mixed woodland, sand forest, riverine forest, rivers and pans, grassland, cliffs, and rocky ridges (Fig. 1). Mkhuze is one of the oldest game reserves in South Africa, with a long and continued tradition of maintaining populations of large mammals. Several ruminant and non-ruminant herbivore species (*e.g.*, elephant, buffalo, rhinoceros, large antelope, and zebra) occur in the reserve, which supports a long list of dung beetle specialist species (Davis 1997). Several studies have already inventoried the dung beetle fauna of the region, especially inside the Mkhuze Game Reserve, where a total of 120 species coexist (Tribe 1976; Doube & Giller 1990; Doube 1991). This long-continued conservation status of the reserve and the high number of diverse mammal species, combined with the mosaic of soil (*i.e.*, from sandy well-drained to clay soils with different proportions between them; Kotze *et al.* 1994) and vegetation cover (*i.e.*, from open woodland to closed canopy areas; Low & Rebelo 1996), makes this reserve the ideal place to test our research question.

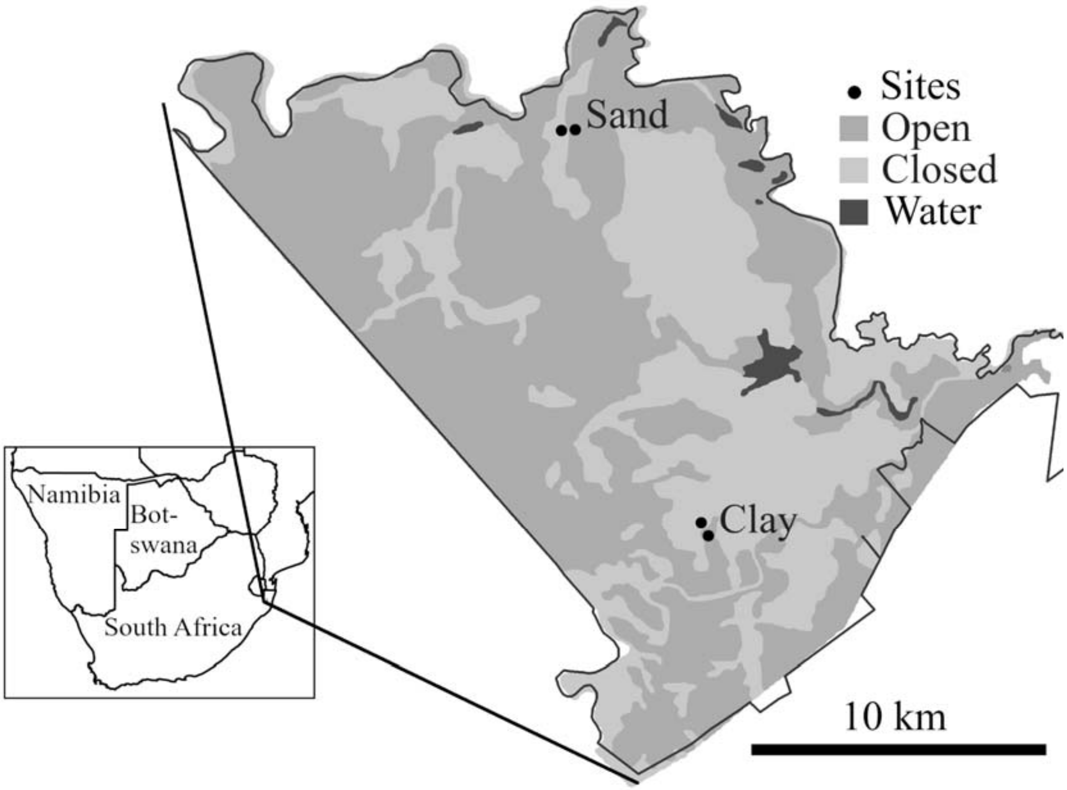

Fig. 1. Location of the study area and types of habitats sampled: (closed) Bush-clay, Open-clay, (closed) Bush-sand, and Open-sand in Mkhuze Game Reserve, KwaZulu-Natal Province, South Africa.

Sampling design

The fieldwork was carried out in December 2016. Dung beetles were sampled from sandy and clay soils under both open woodland and closed canopy areas (for the selection of the areas we used previous categorization of soils – Kotze *et al.* 1994 – and vegetation cover – Low & Rebelo 1996 –, information from park rangers, and knowledge of the authors who have previously sampled in the area), producing a combination of four micro-habitats (Fig. 1), expending one day in each soil type. Samples were taken hourly using pitfall traps from 8:00 to 15:00 (*i.e.*, 7 hours), when day flying beetle activity was at its peak. Nocturnal activity of dung beetles could not be recorded as the combination of darkness and presence of dangerous animals was deemed unsafe for fieldwork. Pitfall traps consisted of 2l plastic buckets approximately 17 cm high and

23 cm in diameter, filled with 250 ml of soapy solution to ensure beetle do not escape. The traps were buried level with the surface of the soil with two rigid wires placed across each trap. Bait consisting of approximately 250 ml of fresh and homogenized cattle dung, wrapped in a 30 cm × 30 cm net cloth, was balanced on top of the wires. Cattle dung was used as it was the bait that was most similar to that produced by most herbivore mammals present in the area. Ten traps per site were placed 50 m apart and on both sides of a road (thus 25 m from the road). The catch of each trap was removed and stored separately. Each trap was provided with fresh bait every hour. Open and closed sites were selected to be 500 m apart to avoid spatial interference during sampling. The total sampling effort was 280 traps/hour. We identified dung beetle species by external morphological and aedeagus comparisons to dung beetle reference collection at the University of Pretoria, former Research Scarab Research Group (now donated to the Iziko Museums of South Africa in Cape Town), Ditsong Museum of Natural History, Pretoria, National Collection of Insects, Pretoria and the National Museum, Bloemfontein. Voucher specimens are housed at the latter museum. Functional groups were assigned using the proposal by Doube (1990).

Climatic variables

At each site, a data logger (HOBO Pendant® Temperature/Light 64K Data Logger) was placed at trap number 5 and set to record temperature (ºC) and relative humidity (%) at intervals of five minutes during the whole time of the study. We calculated average, minimum, and maximum values for each climatic variable based on these values to be used as explanatory predictors. Before that, we used Pearson's correlation coefficient to check the multicollinearity between these variables (Fig. S1). The mean temperature was positively correlated with both minimum and maximum temperature (0.99 for both). Mean relative humidity was positively correlated with both minimum and maximum relative humidity (1.00 for both). We then opted to use both average values. However, both mean temperature and mean relative humidity were negatively correlated (-0.97). Therefore, only mean temperature was used as an explanatory climatic variable in further models.

Statistical analysis

We calculated the sample completeness (coverage) of the dung beetle assemblages per soil type and vegetation cover using a coverage-based estimator (Chao & Jost 2012). The dung beetle data from traps were pooled per site/hour in the analyses. Firstly, we generated sample-size and coverage-based extrapolation and rarefaction curves for each soil type and vegetation cover individually. The sample coverage was obtained by calculating the final slope (coverage) of the species accumulation curves relating to the increase in the number of species with addition of individuals. An integrated sample-size or coverage-based curve includes the rarefaction portion, representing the species increment based on the actual data. The extrapolation portion estimates the species increment beyond the real number of captured individuals (Chao *et al*. 2014). The curves were generated using the *iNEXT* package (Hsieh *et al*. 2016) using Hill numbers of $q = 0$ (species richness).

To test if species composition differed between the type of soil and vegetation cover, we performed a Permutational Multivariate Analysis of Variance Using Distance Matrices (PERMANOVA) (Anderson 2001) and a Multivariate Homogeneity of Groups Dispersions (PERMDISP) (Anderson *et al*. 2006), using the abundance-based Bray-Curtis index as our measure of dissimilarity for both analyses. PERMANOVA partitions compositional distance matrices among sources of variation and fits linear models to distance matrices whilst using a permutation test with pseudo-F ratios to calculate clear effects (Anderson 2001). PERMDISP is the procedure for analysing multivariate homogeneity of group dispersions (variances), an analog of Levene's test for homogeneity of variances. Non-Euclidean distances between objects and group centroids were derived by reducing the original distances to principal coordinates (Anderson *et al*. 2006). PERMANOVA and PERMDISP can be used to rigorously identify location vs. dispersion effects, respectively (Anderson & Walsh 2013). Then, we performed a Non-Metric Multidimensional Scaling (NMDS) to visualize the overall differences in species composition between types of soil and vegetation cover. The PERMANOVA, PERMDISP, and NMDS were run using the R package *vegan* (Oksanen *et al*. 2019).

We analysed the fluctuations in species richness (*i.e*., total amount of species in each habitat combination) and abundance (*i.e*., total amount of individuals in each habitat combination) over time by visually inspecting the graphs and tables. To test the effect of temperature, soil type, and vegetation cover on species richness and abundance, we performed two separate Generalized Least Squares (GLS) models with temporal autocorrelation structures (Zuur *et al*. 2012). GLS models extend the ordinary least squares estimation of the normal linear model by providing for possibly unequal error variances and correlations between different errors. The GLS estimation is commonly used for time-series regression, in which it is generally implausible to assume that errors are independent (Fox & Weisberg 2019). We first tested for different classes of correlation structures (such as 'moving average', 'autoregressive', or 'autoregressive moving average' classes) and selected the best one for each response variable (Crawley 2013): namely: autoregressive moving average process, with orders of 2 for the autoregressive (p), moving average components (q) for species richness and n autocorrelation structure of the order of 1 for species abundance (Pinheiro *et al*. 2018). In both models, temperature, soil type, vegetation cover, and pairwise interaction was used as the explanatory variables. The species richness or abundance per sample (hour) was used as the response variable. We obtained the minimal model through the gradual omission of nonsignificant terms (Crawley 2013). Models were generated using the *nlme* package (Pinheiro *et al*. 2018).

Lastly, to analyse the potential modularity of the network between species and environmental variables, we created a weighted bipartite assemblage preferences network where the sites at each hour constitute one set of nodes (herein spatiotemporal nodes) and the species the other set. A link depicts the presence of a species at given sites at a given time weighted by the number of individuals. We searched for network modules (*i.e.*, groups of nodes densely connected), representing groups of spatiotemporal nodes having similar species composition as well as for the species mainly distributed within these spatial-temporal nodes. We optimized the modularity index proposed by Barber (2007) using the DIRTLPAwb + algorithm (Beckett 2016) as implemented in the R package *bipartite* (Dormann *et al.* 2008). We ran the algorithm 100 times, selecting the network partition providing the best modularity. All the analyses were done in R software (R Core Team 2019).

RESULTS

Assemblage structure and functional groups

In total, we sampled 1439 individuals comprising 27 species and 13 genera (Table 1). The sample completeness was high for all sampled habitats: 0.969 for sand-bush, 0.973 for clay-open, 0.986 for clay-bush, and 1.000 for the sand-open. Clay-open was the poorest habitat site in terms of species and individuals (N=9 spp., 117 ind.). Clay-bush was the habitat with the highest observed species richness and the second-highest total abundance (N=17 spp., 215 ind.). Sand-open was the habitat with the most abundance (N=13 spp., 946 ind.) comprising 4.4 times more individuals than the habitat with the second greatest abundance. The most abundant species that occurred in both clay and sand habitats were *Garreta wahlbergi* (Fåhraeus, 1857) (39.7% in clay; 6.5% in sand) and *Euoniticellus intermedius* (Reiche, 1848) (35.6% in clay; 6.3% in sand), while *Onthophagus aeruginosus* Roth, 1851 (8.5% in bush; 35.3% in open sites)

Table 1. Species of dung beetles collected in different types of soil (clay and sand) and vegetation cover (bush and open) in Mkhuze Game Reserve, Kwazulu Natal Province, South Africa. FG (functional groups): P (paracoprids), T (telecoprids), E (Endocoprids) and in parenthesis Doube (1990) functional groups (I to VII). AC (soil association categories): G (generalists), E (specialists) and (-) no association.

Tribes	Species	FG	AC	Clay		Sand		Total (%)
				Bush	Open	Bush	Open	
Ateuchini	*Pedaria picea* Fåhraeus, 1857	E (VI)	-	2	0	2	0	4 (0.3)
Gymnopleurini	*Allogymnopleurus splendidus* (Bertoloni, 1849)	T (II)	-	2	1	0	0	3 (0.2)
	Garreta wahlbergi (Fåhraeus, 1857)	T (II)	G	98	28	1	71	198 (13.8)
	Gymnopleurus virens Erichson, 1843	T (II)	-	4	2	1	0	7 (0.5)
Oniticellini	*Drepanocerus kirbyi* Kirby, 1828	E (V)	G	7	0	1	11	19 (1.3)
	Euoniticellus intermedius (Reiche, 1848)	E (IV)	G	51	62	3	66	182 (12.6)
Onthophagini	*Kurtops signatus* (Fåhraeus, 1857)	P (VI)	-	8	0	0	0	8 (0.6)
	Onthophagus aeruginosus Roth, 1851	P (IV)	E	0	0	31	372	403 (28.0)
	Onthophagus beiranus Péringuey, 1908	P (IV)	-	0	0	0	4	4 (0.3)
	Onthophagus interstitialis Fåhraeus, 1857	P (IV)	-	2	0	0	0	2 (0.1)
	Onthophagus n.gr. *pullus* Roth, 1851	P (VI)	E	0	0	48	41	89 (6.2)
	Onthophagus pallidipennis Fåhraeus, 1857	P (VI)	-	1	2	0	0	3 (0.2)
	Onthophagus pauxillus D'Orbigny, 1902	P (IV)	E	0	0	26	273	299 (20.8)
	Onthophagus rasipennis D'Orbigny, 1908	P (VI)	G	4	7	1	44	56 (3.9)
	Proagoderus aureiceps (D'Orbigny, 1902)	P (V)	E	0	0	20	7	27 (1.9)

	Proagoderus dives (Harold, 1877)	P (V)	-	0	0	2	0	2 (0.1)
	Proagoderus quadrituber (D’Orbigny, 1908)	P (V)	-	4	0	0	0	4 (0.3)
Scarabaeini	*Pachylomera femoralis* (Kirby, 1828)	T (I)	E	0	0	9	43	52 (3.6)
	Kheper nigroaeneus (Gillet, 1909)	T (I)	E	5	5	0	0	10 (0.7)
Sisyphini	*Sisyphus* (*Neosisyphus*) *calcaratus* Klug, 1855	T (II)	G	12	1	0	5	18 (1.3)
	Sisyphus (*Neosisyphus*) *fortuitus* Péringuey, 1901	T (II)	-	1	0	0	0	1 (0.1)
	Sisyphus (*Neosisyphus*) *mirabilis* Arrow, 1927	T (II)	-	0	0	2	0	2 (0.1)
	Sisyphus (*Neosisyphus*) *rubrus* Paschalidis, 1974	T (II)	-	0	1	3	3	7 (0.5)
	Sisyphus (*Neosisyphus*) *setiger* Roth, 1851	T (II)	-	1	0	1	0	2 (0.1)
	Sisyphus inconspicuus Daniel & Davis, 2018	T (II)	-	2	0	0	0	2 (0.1)
	Sisyphus nanniscus Péringuey, 1901	T (II)	-	4	0	0	0	4 (0.3)
	Sisyphus sordidus Boheman, 1857	T (II)	E	0	0	7	5	12 (0.8)
			Richness	17	9	16	13	27
			Abundance	208	109	158	945	1420

and *Onthophagus pauxillus* D'Orbigny, 1902 (7.1% in bush; 25.9% in open sites) were the most abundant species in both bush and open habitats on the sand.

In terms of the habitats, eight species were exclusive to single habitat combination (Table 1). In contrast, three species (*G. wahlbergi, E. intermedius,* and *Onthophagus rasipennis* D'Orbigny, 1908) were generalist within all habitat combinations. Also, nine species were strongly associated with the soil type independent of the type of cover (Table 1). In terms of soil type, nine species occurred only in sand soils and nine only in clay sites (Table 1). For vegetation cover, *Onthophagus beiranus* Péringuey, 1908 occurred only in open habitats, while 10 species occurred only in bush sites (Table 1). Finally, for temperature, higher number of species and individuals peaked between 9-10 h followed by 10-11 h. Only two species occurred in all hour of sampling: *G. wahlbergi* and *Pachylomera femoralis* (Kirby, 1828). Some species, such as *O. aeruginosus*, *O. rasipennis*, *Kheper nigroaeneus* (Gillet, 1909), *Sisyphus nanniscus* Péringuey, 1901, and *Sisyphus sordidus* Boheman, 1857, occurred only in the morning (7-12h). Besides, *Sisyphus fortuitus* Péringuey, 1901 (10-11 h), *Sisyphus setiger* Roth, 1851 (8-9 h), *Onthophagus interstitialis* Fåhraeus, 1857 (8-9 h), *Proagoderus quadrituber* (D'Orbigny, 1908) (9-10 h), and *Sisyphus inconspicuus* Daniel & Davis, 2018 (9-10 h) were sampled in only one period.

Regarding the functional groups, there was a marked abundance and richness of group II in clay soils, while in sand soils group IV was the most dominant (Fig. S2). Adding the abundances and wealth, group II is the dominant one, oscillating between 9-60%, followed by group IV with a value that oscillates between 11-76%. The group with the lowest values was I, ranging between 2-11%. Group III was not recorded for any habitat or soil. In terms of general patterns, abundance changed strongly between soils and between vegetation cover, while richness remained closer and very similar between habitats for sand soils (Fig. S2).

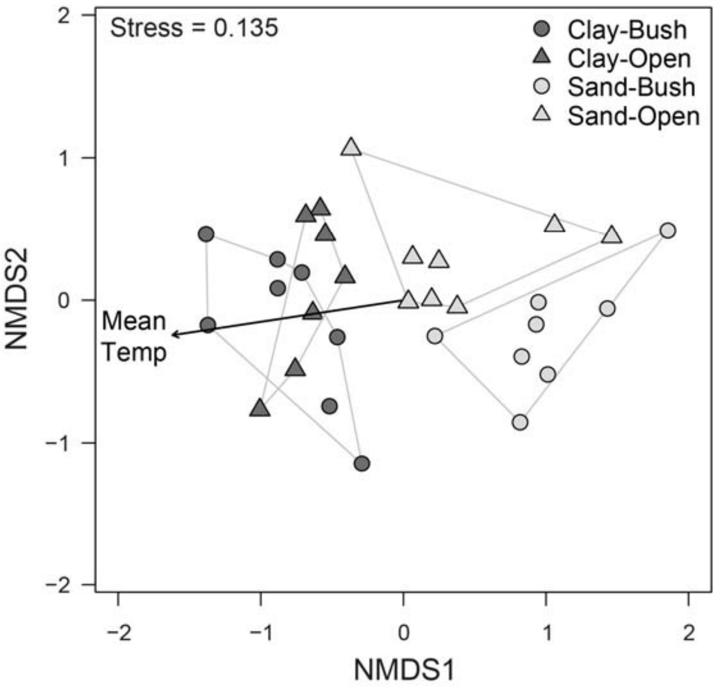

Fig. 2. Non-metric multidimensional scaling of dung beetle assemblages sampled in different soil types (clay and sand sites) and habitats (bush and open sites) in the Mkhuze Game Reserve, KwaZulu-Natal Province, South Africa. We used the Bray-Curtis index as measure of dissimilarity. The colors, symbols, and arrow indicate the main effects of soil type, habitat, and mean temperature (Mean Temp) on dung beetle species composition.

Species composition, richness, abundance vs. environmental variables

Species composition differed between types of soil, vegetation cover, and temperature. Soil type was the most important driver of differences in dung beetle species composition (PERMANOVA: $F_{(1,27)} = 10.361$, $p = 0.001$, $R^2 = 0.225$), followed by vegetation cover (PERMANOVA: $F_{(1,27)} = 4.359$, $p = 0.001$, $R^2 = 0.095$) and mean temperature (PERMANOVA: $F_{(1,27)} = 4.308$, $p = 0.001$, $R^2 = 0.094$) (Fig. 2). Higher mean temperatures were found in open-clay habitats (mean=38,30ºC; min=27,62ºC; max=45,07ºC) and lower mean temperatures were found in the open-sand habitats (mean=32,78ºC; min=24,08ºC; max=39,06ºC). The highest temperature was in bush-clay (48,57ºC) and the lower in open-sand (24,08ºC). PERMDISP analyses also showed differences in the group's dispersion for types of soil ($F_{(1,29)} = 4.437$, $p =$

0.044, Fig. S3a), but not for vegetation cover ($F_{(1,29)} = 3.187$, $p = 0.084$, Fig. S3b). Therefore, in addition to showing differences in species composition between soil types, sand habitats had a greater heterogeneity in dung beetle composition among themselves, regardless of the type of vegetation cover (Fig. S3a).

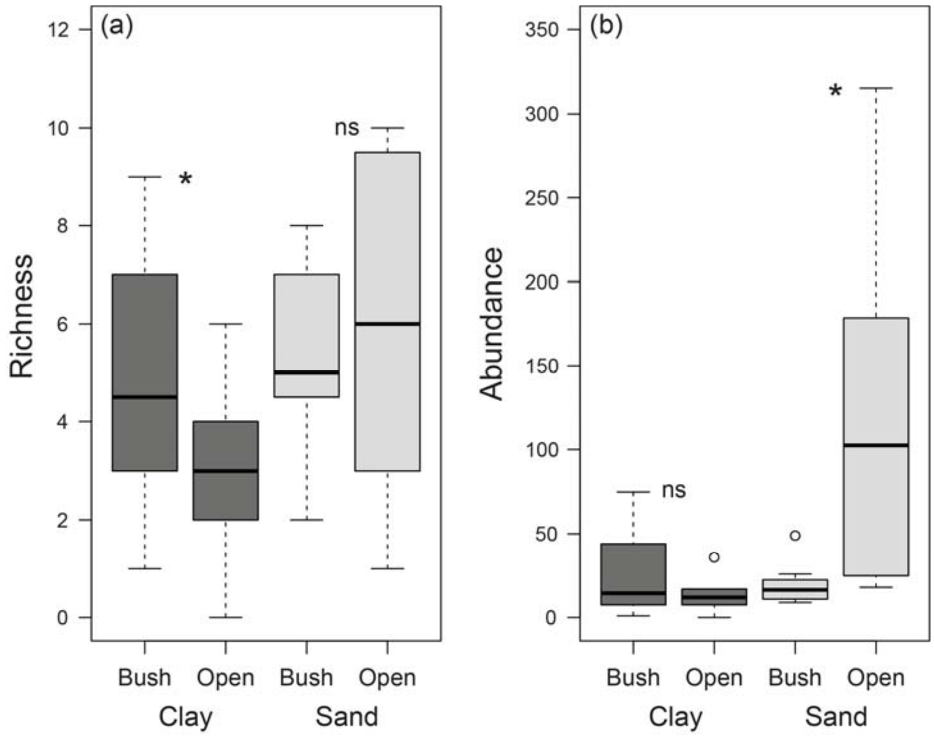

Fig. 3. Species richness (a) and abundance (b) of dung beetles sampled under different vegetation cover (bush and open) and in two soil types (clay and sand) of Mkhuze Game Reserve, KwaZulu-Natal Province, South Africa. Asterisks (*) indicate statistical differences and 'ns' indicates no statistical differences according to generalized least squares regressions. White circles represent outliers.

Table 2. Results of full and minimal models of generalized least-squares regression on species richness and abundance of dung beetles in Mkhuze Game Reserve, KwaZulu-Natal Province, South Africa.

Richness	**Full model**	**d.f.**	**$F_{(1,25)}$**	**p-value**
	Intercept	1	46.317	**<0.0001**
	Soil	1	0.292	0.594
	Vegetation cover	1	0.036	0.851
	Mean temperature	1	6.148	**0.020**
	Soil : Vegetation cover	1	5.653	**0.025**
	Soil : Mean temperature	1	0.000	0.996
	Vegetation : Mean temperature	1	0.160	0.693
	Minimal model	**d.f.**	**$F_{(1,27)}$**	**p-value**
	Intercept	1	58.207	**<0.0001**
	Soil	1	0.310	0.582
	Vegetation cover	1	0.045	0.833
	Mean temperature	1	7.303	**0.012**
	Soil : Vegetation cover	1	6.709	**0.015**
Abundance	**Full model**	**d.f.**	**$F_{(1,25)}$**	**p-value**
	Intercept	1	2.349	0.138
	Soil	1	0.419	0.523
	Vegetation cover	1	4.062	0.055
	Mean temperature	1	0.646	0.429
	Soil : Vegetation cover	1	4.237	**0.050**
	Soil : Mean temperature	1	0.973	0.334
	Vegetation cover : Mean temperature	1	1.171	0.290
	Minimal model	**d.f.**	**$F_{(1,28)}$**	**p-value**
	Intercept	1	1.915	0.177
	Soil	1	0.311	0.582
	Vegetation cover	1	4.133	0.052
	Soil : Vegetation cover	1	4.586	**0.041**

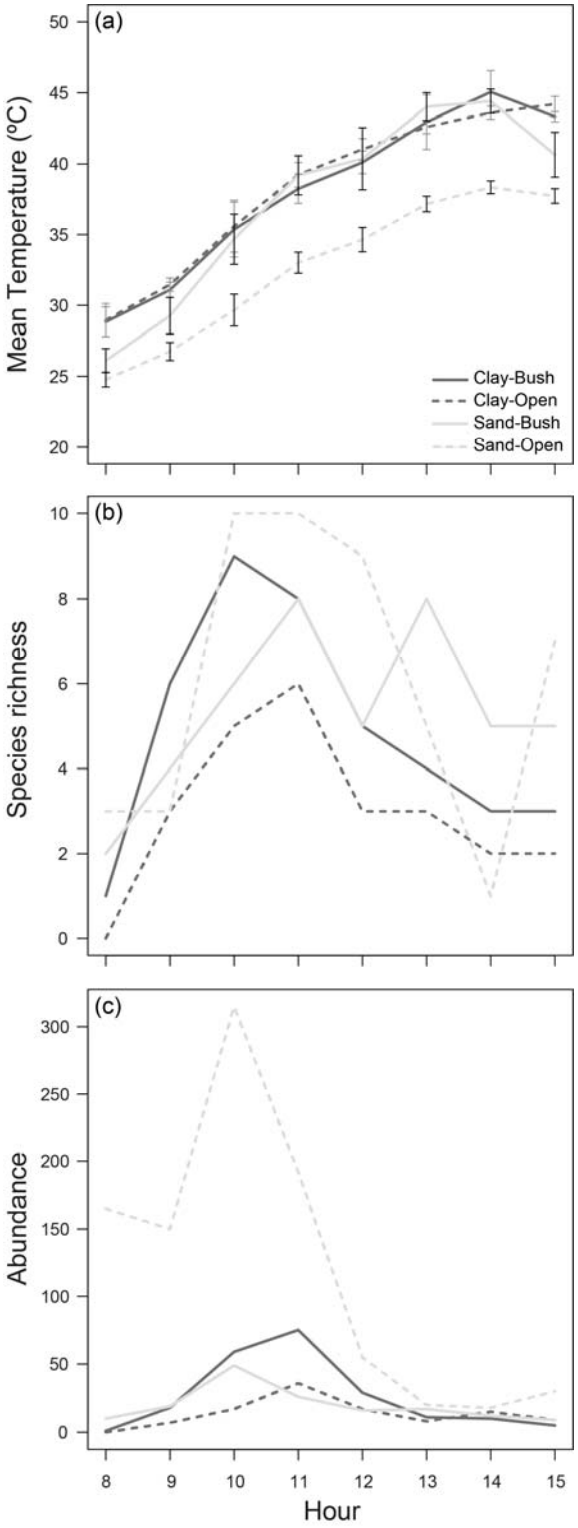

Fig. 4. Mean temperature (± standard deviation) (a), species richness (b), and abundance (c) of dung beetles sampled under different vegetation cover (bush and open) and in two soil types (clay and sand) in Mkhuze Game Reserve, KwaZulu-Natal Province, South Africa.

Species richness was influenced by interactions between soil type and vegetation cover and also by mean temperature regardless of the soil type and vegetation cover (Table 2). High mean values of richness were found in the bush vegetation of clay soils, and no differences in species richness were found between vegetation conditions on sand soils (Fig. 3a). Richness showed an overall increase up to 11:00 (temperature between 33 and 39ºC) followed by a general decrease with increasing temperatures (up to 38 and 45ºC) (Fig. 4). Abundance showed a peak for individuals at 10:00 for sandy soils and 11:00 for clay soils but was not influenced by temperature. Dung beetle abundance was also influenced by interaction between soil type and vegetation cover but not with mean temperature (Table 2). High mean values of abundance were found in open vegetation only for sand soils (Fig. 3b).

Modularity of assemblage preferences network

The modularity network analysis between species and environmental variables reports six modules (spatiotemporal nodes, Fig. 5). Twelve species formed the first module (*e.g.*, including *O. pauxillus*, *P. femoralis*, *Proagoderus aureiceps* (d'Orbigny, 1902)) were associated with bush and open-sand from 9:00 to 14:00 h. The second module was formed by only three species associated with bush-clay from 8:00 to 9:00 h. A third module was formed by four species (*e.g.*, including *E. intermedius*) with a wide spectrum of habitat associations, including bush and open-clay and open-sand from 9:00 to 15:00 h. Seven species formed a fourth module (*e.g.*, including *G. wahlbergi*, *Sisyphus calcaratus* Klug, 1855) and were associated mainly with bush-clay and open-clay from 7:00 to 15:00 h. A fifth small module was formed by two species exclusively associated with open-clay from 8:00 to 9:00 h. Finally, a sixth module was formed by two species strongly associated with bush and open-sand from 7:00 to 9:00 h. Also, in these modules, we identified particular species that are dominant in each node [*e.g.*, *O. pauxillus* (sand specialist; Mod. 1), *Kurtops signatus* (Fåhraeus, 1857) (clay-bush specialist; Mod. 2), *E.*

intermedius (generalist species; Mod. 3), *G. wahlbergi* (generalist species; Mod. 4), *O. rasipennis* (generalist species; Mod. 5), and *O. aeruginosus* (sand specialist; Mod. 6)].

DISCUSSION

We evaluated the influence of soil type, vegetation cover, and temperature on species diversity and functional structure of dung beetle assemblages in different habitats in South Africa. In general terms, we corroborated our study hypothesis in finding that the combination of microenvironmental variables strongly influenced diversity and structure of the dung beetle assemblage. The main result showed an interacting effect of local scale resources and conditions in space and time related to biotic and abiotic preferences such as: i) vegetation cover, ii) soil type, and iii) diel activity. In this sense, the combination of all these preferences acts as a potential dilution mechanism of interspecific competition in saturated habitat conditions with ephemeral resources, generating a modular structure in terms of the assemblage composition.

Dung beetle diversity and structure vs. environmental variables

KwaZulu-Natal is a well-known centre of biotic endemism (Van Wyk 1990), presenting a high heterogeneity between habitat types (*i.e.*, different types of soil; Van Rensburg *et al*. 1999) which directly affects the structure and diversity of dung beetle assemblages. Our results point out that soil type is the most critical habitat determinant for several species found in this locality, coinciding with previous studies (Davis 1996b; Doube 1983). In an early work, Nealis (1977) proposed that soil type is a significant determinant in the distribution of dung beetles in Texas, USA. Later, in a study located in Hluhluwe Game Reserve near Mkhuze Game Reserve, Doube (1983) found that soil type influenced the relative abundance of various species. Subsequently in Mkhuze Game Reserve, Osberg *et al*. (1992) determined that for *Allogymnopleurus splendidus* (Bertolini, 1849) and *Allogymnopleurus consocius* (Péringuey, 1901), the association with sand and clay soils is more important than the influence of vegetation cover. In Gauteng, Davis (1996c) studied dung beetle preferences for different types of soil and the relationship between functional groups. Davis (1996c) reported no differences in abundance between sand and clay in contrast with our results (sand: N=1107, 76.93% and clay: N=332, 23.07%), but also recorded differences in biomass, finding a much greater value on sand which agrees with our findings.

In South America, Silva *et al*. (2015) found that the concentration of clay in the soil influences the structure of dung beetle functional groups at the micro-habitat level. For instance, small tunnellers and rollers are most affected by variation of the soil granulometry in a semideciduous forest in western Brazil. The increase in clay concentration led to a reduction in small paracoprids and an increase in small telecoprids. Farias & Hernández (2017) also found strong associations of dung beetle functional groups with different soil conditions in four agroecosystems (corn, bean, sugarcane, and cattle pastures) in southern Brazil. For instance, occurrence of the tunneller *Dichotomius nisus* (Olivier, 1789) and the dweller *Trichillum externepunctatum* Preudhomme de Borre, 1880 correlated positively with organic matter content whereas the roller *Canthon chalybaeus* Blanchard, 1845 correlated positively with soil texture, preferring sandier soils. In both African and South American studies, it is evident that species preference for a specific soil type is a clear reflection of edaphic structural differences and climatic history throughout geological periods (Davis *et al*. 2016).

The association with a particular type of soil may play an essential role as a segregation mechanism for interspecific competition, reducing the number of species that potentially interact. Our results concur with the findings of Doube (1991), especially in the strong association with specific soil types shown by some species such as *P. femoralis* or *S. sordidus*, which prefer sandy soils. Doube (1991) also found that dung beetle assemblage structure is more influenced by soil type than by vegetation cover. Doube (1991) also reported that large rollers were more dominant on sandy soils so that this type of soil had the highest dung beetle biomass. Osberg *et al*. (1993) proposed that soil type (*i.e*., texture, moisture, and hardness) could affect dung burial (*i.e*., burial behaviour, number of brood balls, and burial depth). However, it is important to consider that a particular type of soil has a direct effect on the vegetation cover that an area can maintain and affects the presence and abundance of the related mammal fauna, becoming a complex synergistic system of relationships as shown in Davis & Scholtz (2020).

Halffter & Arellano (2002) stated that vegetation cover is a determining factor for dung beetle distribution after evaluating the effects of deforestation on dung beetles in Mexico. Forested- (or bush-) and open-vegetation areas may support different species compositions as a result of distinct local conditions such as differences in temperature and soil. In this context, it is essential to note that dung beetles build their nests in the soil or at the dung-soil interface (Halffter & Edmonds 1982). Besides, different vegetation types may be a result of soil conditions, which may be more important than type of vegetation *per se* for dung beetle species distribution, as shown here. Locally, the climate experienced by a species is a key determinant of population growth and an important variable of the fundamental niche space (Hutchinson 1957). Microclimates can differ markedly between different types of habitats (Geiger *et al*. 2003), where vegetation cover substantially reduces solar radiation at the soil and lowers the temperature compared to open environments (Oliver & Morecroft 2014). Furthermore, the average and maximum temperature in some sites reached 40–42ºC or more, a maximum tolerated temperature that generates strong physiological flight constraints (Verdú *et al*. 2006). This can explain the decrease in species richness and abundance after midday. Solar radiation has been acknowledged as one of the most influential factors determining dung beetle activity (Lobo *et al*. 1998). Thermal tolerance and thermoregulation mechanisms are important in determining the patterns of habitat association and daily activity of dung beetles (Giménez

Gómez *et al*. 2018). Hence, the combination of soil, vegetation, and microclimatic conditions besides food availability, jointly determines the distribution of dung beetles.

Modularity of assemblage preferences network

The modularity analysis between species and environmental variables shows a robust assemblage preferences network, demonstrating that species have a strong association with the habitat, and time of the day. We found several network modules that represent a potential separation of groups of species coexisting in space and time, which could affect their interaction and possibly reduce competition between functional groups. From 27 species we recorded in Mkhuze Game Reserve, just 17 (in the richest habitat combination - clay-bush) coexist in space but not in time. In this sense, the interaction and hypothetical competition inside each of these modules (*i.e*., spatial-temporal nodes) could be elevated. It is essential to point out that in each of the modules, we found a mix of different functional groups. Even in those nodes with only two species (*e.g*., Mod. 5 and 6), each species was from a different functional group (*i.e*., paracoprids and telecoprids). It is also important to clarify that these modules are strongly conditioned by the presence of a species in a given habitat at a given time weighted by the number of individuals. Network modularity has been studied in other groups and in different contexts (Kirmse & Chaboo 2020; Noriega *et al*. 2020; Ramos-Robles *et al*. 2020) but, to our knowledge, this is one of the first studies of dung beetles that uses such an analysis to understand the structure of the assemblage.

It is worthwhile to note that no analysis was conducted on activity by nocturnal members of the assemblage. Nocturnal species might have very different responses and trends to those observed for diurnal species. Furthermore, our results might have been affected by the seasonal activity since the pattern herein described reflects only a portion of the rainy season. It would be fascinating to include the whole spectrum of seasonal activity. We are also aware that the use of only one type of bait (*i.e.*, cattle dung) in our study may have biased the response of some species due to specialised preferences for dung type resources, as evidenced in other studies (Doube 1983; Tshikae *et al*. 2008; Davis *et al*. 2010).

Future research should evaluate and quantify a possible relationship between these environmental variables and some functional traits and functions (*e.g.*, de Castro-Arrazola *et al*. 2020). We thus recommend the use of different types of bait (*e.g.*, local wild animals) under continued short (24-hour sessions, including night activity) and long (seasonal) temporal regimes to better understand the potential variation between conditions and to understand if the importance of the microclimatic variables that we identified locally are equally relevant at a regional scale. In this sense, the use of local excrements may attract some specialized species and show differences in the recorded pattern. Additionally, as our results are associated with a conservation area, it would be interesting to compare them with other regions with different anthropogenic disturbance regimes. Finally, we found that the combination of microenvironmental preferences strongly influenced the dung beetle assemblage diversity and functional structure, acting as a dilution mechanism of interspecific competition in saturated habitat conditions and generating a modular network structure of the assemblage.

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AUTHOR CONTRIBUTIONS

GMD and ALVD conceived and designed the study. CHS and CLS contributed to the funding acquisition. GMD, JAN, ALVD, and CMD carried out the experiments and the fieldwork. GMD, PGS, and JAN performed the analysis, interpreted the results, and designed the figures. GMD and JAN drafted the manuscript with input from all authors. All authors contributed to the final manuscript.

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