Biological Conservation 260 (2021) 109211

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Replacing native mammal assemblages with livestock in African savannahs, impacts dung beetle diversity and reduces body size

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ARTICLE INFO

Keywords:
Dung beetles
Land-use
Scarabaeinae
Trophic interactions
Mammals
African savannah

ABSTRACT

Replacement of complex assemblages of native mammal fauna with livestock species reduces niche heterogeneity. This negatively affects taxa such as dung beetles, which depend on them and can, in turn, affect ecosystem functioning. We assessed the response of dung beetle diversity, biomass and body condition to cattle-farming pressures in protected areas (PAs) and adjacent farms in the savannah biome of northern Namibia. We hypothesized that rich native mammal assemblages are essential to maintain dung beetle diversity and overall biomass. We further explored whether the low-quality dung resources on farms would lead to a decrease in individual body size for species found on both farms and PAs. Overall dung beetle richness increased with higher mammal richness but not relative abundance, demonstrating that a rich native vertebrate assemblage promotes dung beetle richness. Overall dung beetle biomass was lower on farms, but abundance showed no difference. Large-bodied dung specialist species, which are known to be functionally superior, were absent on farms while smaller generalist species proliferated. Furthermore, a large proportion of individuals of species common to both farms and PAs were physically smaller on farms, indicating reduced body condition. Our results show that a high diversity of native mammals maintains dung beetle diversity and higher biomass on PAs. A decrease in native dung on farms leads to reduced body mass, likely negatively impacting ecological function. These results suggest that the conservation of dung beetles and their functions in the expansive African savannah ecosystems is dependent on a complex mix of native mammal species.

1. Introduction

Land transformation for livestock grazing accounts for nearly 60% of the world's agricultural land and has severe consequences for native biodiversity (Alkemade et al., 2013; Newbold et al., 2015; Cardoso et al., 2020; Samways et al., 2020). Rangelands such as savannah ecosystems contribute the bulk of this forage but support a disproportionally high diversity of native mammal herbivores (Veblen et al., 2016). Replacing native mammals with livestock may maintain a portion of native biodiversity, but stocking densities are often too high and domestic grazers usually replace nearly all larger mammals, altering normal ecosystem processes (Young et al., 2018; Filazzola et al., 2020). Studies of the effect of livestock farming in African savannahs have focused on native vertebrates (Young et al., 2018) or vegetation (Wilkerson et al., 2013), largely ignoring arthropods (Filazzola et al., 2020). This despite arthropods providing many essential ecosystem functions (Noriega et al., 2018; Samways et al., 2020) and are considered good environmental indicators (McGeoch and Chown, 1998). One of the most widely used indicator arthropod taxa are dung beetles (Nichols et al., 2008) as they have a long co-evolutionary history with mammals (Nichols et al., 2009; Sole and Scholtz, 2010), provide keystone ecological functions such as dung removal, seed dispersal and the regulation of pests and diseases (Andresen and Levey, 2004; Nichols et al., 2008) and are sensitive to changes in biotic and abiotic conditions (Davis et al., 2008). They are therefore an ideal focal taxon to explore the effects of land-use change on savannah ecosystems (Nichols et al., 2008; Raine and Slade, 2019).

Mammal species identity and relative abundance are important to preserve ecological integrity in savannah ecosystems (Pryke et al., 2016). Even so, few studies have explored how mammal species compositional changes affect dung beetle assemblages (Raine et al., 2018; Raine and Slade, 2019; Valiente-Banuet et al., 2015). Selective defaunation and replacement of wild large mammals with livestock could lead to the extinction of more specialised mammal-dung beetle interactions and rapid ecosystem functional losses (Nichols et al., 2009; Culot et al., 2013). However, most dung beetles seem to be dung

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https://doi.org/10.1016/j.biocon.2021.109211
Received 14 December 2020; Received in revised form 27 May 2021; Accepted 3 June 2021
Available online 17 June 2021
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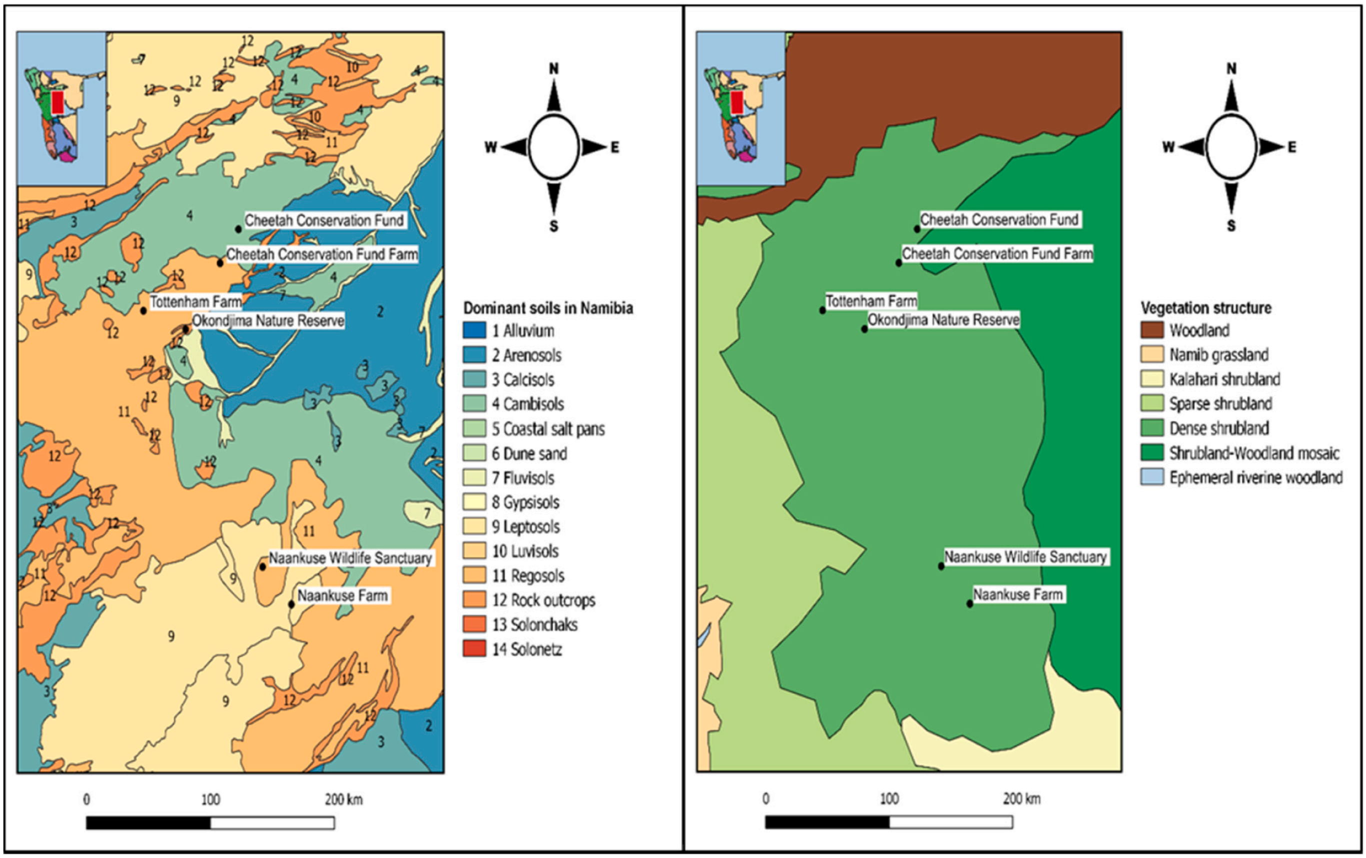

Fig. 1. Map indicating the location of sites in relation to a) dominant soil profile and b) vegetation structure. The shapefiles for the maps are available online form the Digital Atlas of Namibia project at http://www.uni-koeln.de/sfb389/e/e1/download/atlas_namibia/main_namibia_atlas.html

generalists and may be able to readily adapt to altered resources (Hanski, 1991; Holter and Scholtz, 2007). Some generalists may even select for the abundant newly introduced resources due to resource conditioning (Tshikae et al., 2008; Scholtz et al., 2009) and mitigate some functional losses by reductions in specialists.

Resources high in nitrogen benefit dung beetle development and ultimately reproductive performance (Hanski, 1991). Mean percentage of nitrogen in native herbivore dung in African savannah (Codron et al., 2006) is higher than that of livestock (mainly cattle) (Augustine, 2003). Dung quality from livestock is further reduced by using veterinary medical products (Hammer et al., 2016; Verdú et al., 2018) which affects dung beetle communities (Scholtz et al., 2009). Resource quality has multiple effects on the biology of individual dung beetles, and dung beetle body size (or mass) can be used as a proxy for its cumulative effects (Gittings and Giller, 1998). Larger individuals are generally more fit as they are stronger competitors for food resources and mates (Larsen et al., 2008; Nervo et al., 2014; Tonelli et al., 2017). Therefore, even if a species can adapt to altered resources, the body condition of individuals may be severely compromised (Salomão et al., 2018; Villada-Bedoya et al., 2019). Decreased body size has negative effects on ecosystem functions and services (Larsen et al., 2008; Scholtz et al., 2009; Tonelli et al., 2017). Despite the close link between dung beetle size, resource parameters (quantity and quality of dung) and ecosystem function (Holter and Scholtz, 2007; Schwab et al., 2016), there is a dearth of studies evaluating the impact of replacing native mammals with livestock on dung beetle development. Also, few studies have incorporated changes in dung beetle body condition in relation to changes in ecological parameters, and those that have only evaluated a few species (Slade et al., 2007; Manning et al., 2016). General patterns for an entire assemblage have yet to be assessed.

Here, we determined whether livestock can act as effective surrogates for wild mammals in an African savannah ecosystem. We compared dung beetle diversity and biomass and the body condition (mass) of individuals between protected areas (PAs) and cattle farms. We tested the hypothesis that less diverse native mammal fauna on farms will lead to decreased dung beetle richness and altered community assemblage composition. We postulate that dung beetles would show a greater preference for dung originating from native grazers than for dung from domestic livestock due to a long co-evolutionary history. This effect may be diminished on farms due to the prevalence of generalists and resource conditioning. Total dung beetle abundance and biomass was expected to be higher on farms (due to generally higher availability of dung), but mean mass of individuals of remaining species would be lower due to decreased quality of livestock dung resources.

2. Methods and materials

2.1. Study region

This study was conducted in northern Namibia, a region dominated by thornbush savannah on Regisols soils (Fig. 1). Minimum summer temperatures vary between 15 and 17 °C and maximums often exceed 40 °C. Rain is restricted to summer (100 mm–300 mm) but is highly erratic (Barnard et al., 1998). The landscape consists of a mosaic of cattle farms (Brahman and Simmentaler breeds) and protected areas (PAs). Dung beetles were sampled from three PAs (Okonjima Nature Reserve, N/a'an ku sê Lodge, and the Wildlife Sanctuary and Cheetah Conservation Fund) and three farms adjacent to these (Tottenham, N/a'an ku sê and Cheetah Conservation Fund Livestock Farms) (Fig. 1). These PAs maintain the natural complement of native mammals such as elephant, wildebeest, rhino, lion, giraffe and other iconic African fauna while these mammals are largely absent from farms (van Schalkwyk et al., 2010). The minimum distance between a farm and PA pair (region) was 17 km and maximum distance between pairs was 70 km. Ten sites were selected at each estate (farm or PA) with the help of managers, field guides and farmers that had intimate knowledge of the major soils, vegetation physiognomies and grazing intensities on their respective properties. These variables were kept as consistent as possible to minimise their effect on dung beetles collected. Sites at each estate were a minimum of 1 km apart to avoid pseudoreplication (Silva and Hernández, 2015). Therefore, our sampling design included 3 regions × 2 biotopes (farm and PA) × 10 sites = 60 sites in total.

2.2. Dung beetle collection

At each site, dung beetles were sampled using four baited pitfall traps set >100 m apart forming a square to minimise trap interference from the intermixing of bait odours (Flechtmann et al., 2009). Traps consisted of a 2 L plastic bucket (17 cm diam., 14 cm deep) that was buried with the rim flush with the soil surface and half-filled with soapy water to capture beetles. Traps were baited with fresh dung balls (150 g) of either wildebeest, collected from Okonjima Nature Reserve, or cattle dung, collected from Tottenham Farm, wrapped in nylon and suspended over the trap (Pryke et al., 2016). All baits were homogenised and then frozen (−20 °C) until use. This was done to ensure consistency in attractiveness. Each site had two plots with two traps baited with either wildebeest or cattle dung. Traps were operational for 24 h after which baits were replaced with fresh dung and left operational for another 24 h. The entire sampling protocol was repeated in the early rainy season (December/January) and in the late rainy season (March/April).

Collected dung beetles were sorted, counted and identified to the lowest taxonomic rank possible using published keys (Appendix A). Species were also assigned to a functional guild according to their method of dung use as endocoprids, paracoprids or telocoprids using this literature.

2.3. Mammal richness and relative abundance

The identity and relative abundance of medium to large mammals (larger than a rabbit) at each site were determined using dung transects as recommended for savannah ecosystems (Marques et al., 2001; Sensenig et al., 2010). All dung piles were identified and counted along a combined transect of 1 km long and 4 m wide, divided into four sub-transects of 250 m that radiated in opposite directions at the same sampling sites where dung beetles were being sampled. Seven days later, only newly deposited dung along these transects were recorded. The total number of species recorded per transect during both surveys were used as an estimate for mammal richness and the mean number of dung pads per transect between both surveys were used as an estimate of mammal relative abundance at each site during the sampling period (Cromsigt et al., 2009). Irrespective of which method used, not all species and individuals present at sites during sampling will be recorded (Bogoni et al., 2019; Raine and Slade, 2019).

2.4. Dung beetle mass

The mean mass per individual of each dung beetle species was determined from a random selection of 10 individuals per species collected from the farms and the PAs respectively (20 in total when available, otherwise all available individuals). Total body length was measured (linear distance between the pygidium and the clypeus) and the body length was then used to calculate mass using the formula: $\text{Biomass} = 0.010864 \times \text{Length}^{3.316}$ (Lobo, 1993; Tonelli et al., 2020). This formula was devised specifically for calculating dung beetle biomass by using a log-log regression technique to give the dry mass of the dung beetle in milligrams (Lobo, 1993; Tonelli et al., 2020). After the biomass of each species was calculated, the mean biomass of each species (mean of the 10 individuals measured) was multiplied by the total number of beetles for each species to determine the total biomass sampled for each species. These calculations were also done for each land-use type, bait type and nesting type.

2.5. Data analyses

Data for the two collection seasons were combined per dung type per site for all analyses. Therefore, for analyses we effectively had 120 independent samples for comparisons structured as: 3 regions × 2 biotopes (farm and PA) × 10 sites × 2 dung types = 120 samples in total. Relative completeness of sampling was estimated using EstimateS 9.1 (Colwell, 2013). The non-parametric abundance-based estimators, Chao 2 and Jackknife 2 were calculated using 100 randomizations of the total abundance of beetles collected per site (Chao et al., 2004). All other statistical analyses were conducted using R3.6.1 (R Development Core Team, 2019).

Dung beetle abundance, richness and biomass were checked for best-fit distribution using quantile-quantile plots for normal, Poisson, negative binomial or gamma families. When the spatial random variable of site was added to the models it improved spatial independence in a correlogram using the package *ncf* (Bjørnstad, 2020). The variable "site" represents four pitfall traps with two different dung types, with the two traps baited with the same dung type pooled for the analyses. Mammal richness and relative abundance data were compared between farms and PAs using generalized linear mixed models and the *lme4* package with a negative binomial distribution and site as a random variable (Zuur et al., 2009; Bates et al., 2015). The effect of land-use, bait type, mammal richness, mammal relative abundance and the interaction between land-use and bait type on dung beetle abundance, richness and biomass were evaluated using a model averaging technique. All variables were first rescaled and then checked for multicollinearity using the variance inflations factors (VIF) in the *car* package (Fox and Weisberg, 2019). All variables had a $\text{VIF} < 4$. Global GLMM models containing these variables and the random factor of site were created with Poisson distribution for species richness data, negative binomial distributions for abundance data and log-normal for biomass data. Models containing all possible combinations of variables and the null model were then ranked for best fit of the environmental variables, based on the AICc criteria using the dredge function in *MuMIn* (Bartoń, 2019). The best fitting model and models with ΔAICc of ≤ 4 were averaged using the model.avg. function in the *MuMIn* package. Significant interactions between land use and bait type had their means compared using Bonferroni corrections using the *multcomp* package (Hothorn et al., 2008).

Compositional responses of dung beetle assemblages to differences in land-use type, bait type, mammal richness and relative abundance were assessed using the *mvabund* package in R (Wang et al., 2012). The *manyglm* function was used to build multivariate GLMs of candidate models. This function fits multiple generalized linear models on all combinations of variables between a community and environmental data set, thus allowing effects to be identified at the assemblage level (Wang et al., 2012). These analyses assumed the predictors' responses to be correlated and so calculated via ridge regularization (using the "shrink" parameter). All these multivariate models were fitted with a negative binomial distribution, as well as the region to account for spatial autocorrelation, assuming a quadratic mean-variance. Test statistics were calculated based on the "pit-trap" resampling method with 999 permutations (Wang et al., 2012). Pairwise multivariate GLM for the overall, roller, tunneller and dweller assemblages were based on the combined effects of land use and bait types.

We tested for differences in the mass of dung beetle species between farms and PAs for species that we collected more than ten individuals at each land-use type. Data on estimated individual mass for ten individuals from each land-use ($n = 20$ individuals in total) was first tested for normality using Shapiro Wilk's tests ($P < 0.05$) where after a Mann-Whitney *U* test was performed in R. Hereafter all P-values were adjusted for multiple testing using a Bonferroni corrective model (Sokal and

Table 1
Summary results of generalized linear mixed models across all sites (n = 120) for the effects of land use, bait type, mammal richness and mammal relative abundance on dung beetle richness, abundance and biomass. Only those variables retained after model selection procedure based on ΔAICc are shown. The R^2 value represents variance explained by the explanatory variables.

Response variable	R^2	Predictor variable	df	F-value	P-value
	0.75	**Land use**	**1**	**3.13**	**0.002**
		Bait type	1	0.23	0.819
		Mammal richness	1	1.85	0.065
		Mammal relative abundance	1	0.99	0.324
Species richness		**Land use * Bait type**	**3**	**3.84**	**<0.001**
	0.26	**Land use**	**1**	**2.41**	**0.016**
		Bait type	1	1.60	0.110
		Mammal richness	1	0.14	0.886
		Mammal relative abundance	1	0.25	0.801
Abundance		Land use * Bait type	3	1.58	0.114
	0.20	Land use	1	1.45	0.146
		Bait type	1	0.93	0.353
		Mammal richness	1	1.94	0.054
		Mammal relative abundance	**1**	**2.01**	**0.044**
Biomass		Land use * Bait type	3	1.73	0.083

Rohlf, 1995). To determine if there was a general trend for dung beetles to differ in mass between farms and PAs, a likelihood ratio (G-test) was performed using the same candidate species evaluated above. Species were scored as larger in either PAs or farms based on their mean mass and the ratio was tested against what was expected at random (50:50 ratio) using the *DescTools* and *RVAideMemoire* packages in R (Mangiafico, 2015). Finally, indicator value (IndVal) analyses were performed to identify species that were associated with protected areas or farms, as well as those that prefer either cattle or wildebeest dung (Dufrene and Legendre, 1997), using the *labdsv* package in R (Roberts, 2019). This method combines the relative abundance and frequency of occurrence of each species to different habitat associations.

3. Results

In total, 70,540 individuals representing 101 species and morphospecies from the Scarabaeinae (85 species) and Aphodiinae (16 species) were collected (Appendix B). This was in line with total species richness expected (Appendix C). Approximately 80% of individuals were represented by only seven species. Ninety-eight species and 44,432 individuals were sampled from PAs while 75 species and 26,108 individuals were recorded on farms. PAs harboured 26 unique species while farms only had three unique species. Of the rare species, *Onitis bilobatus* (Ferreira) represents a species previously known only from the

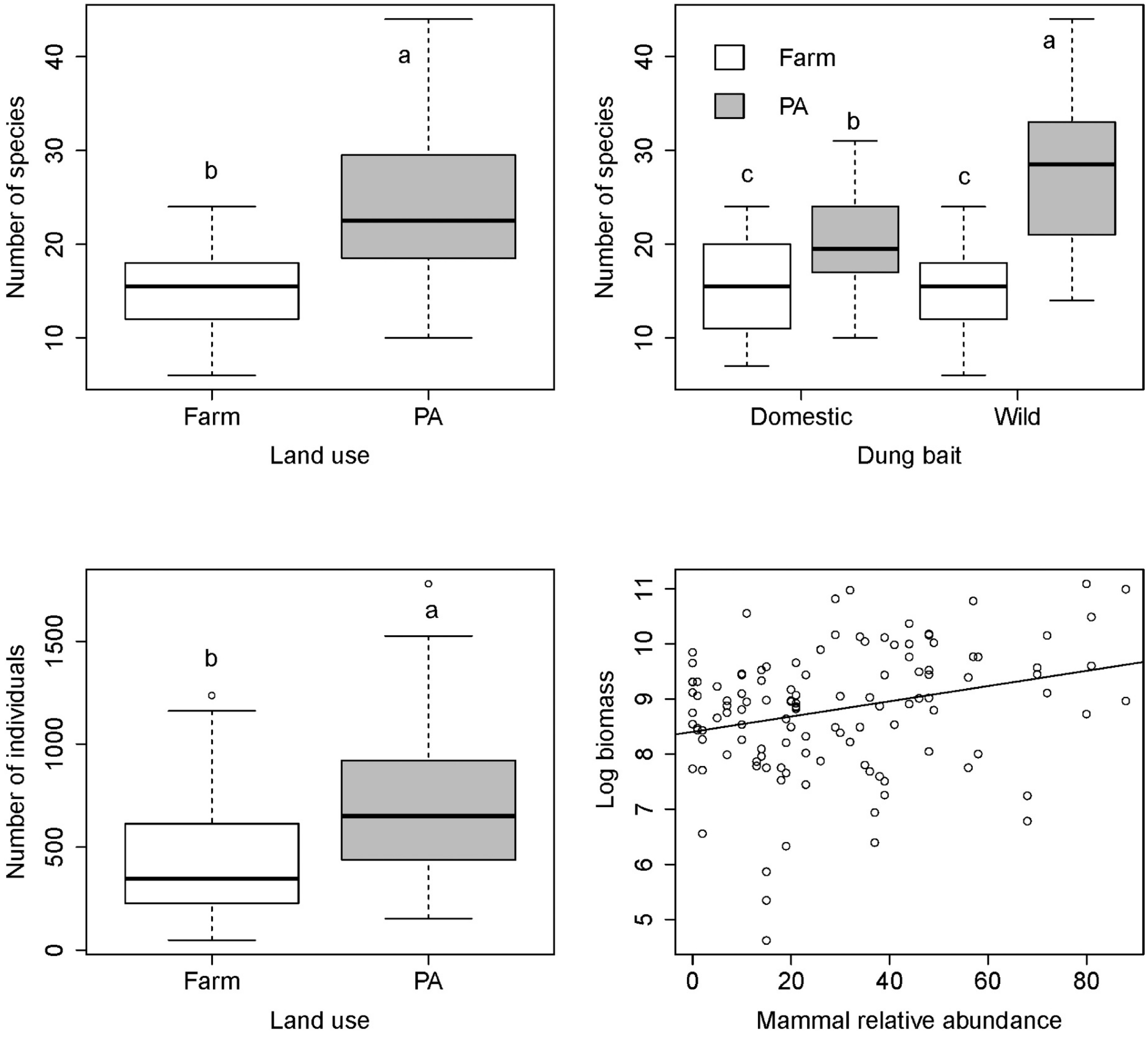

Fig. 2. The significant responses for the overall dung beetle species richness, abundance, and biomass. Different letters above means represent significant differences between means after a Bonferroni correction.

Table 2

Summary results of generalized linear mixed models across all sites ($n = 120$) for the effects of land use, bait type, mammal richness, mammal relative abundance and the interaction between land use and bait type on dung beetle richness, abundance and biomass per nesting guild (rollers, tunnellers and dwellers). The R^2 value represents variance explained by the explanatory variables. Only those variables retained after model selection procedure based on ΔAICc are shown.

Response	R^2	Land use	Bait type	Mammal richness	Mammal abundance	Land use * bait type
		df = 1	df = 1	df = 1	df = 1	df = 3
Roller richness	*0.12*	0.01	0.25	**2.15***	1.07	**2.01***
Roller abundance	*0.13*	1.48	0.81	0.21	1.30	1.03
Roller biomass	*0.09*	**2.49***	0.02		1.17	0.94
Tunneller richness	*0.37*	**3.87*****	0.72	0.89	1.37	0.81
Tunneller abundance	*0.17*	**2.51***	1.74	1.36	0.75	0.45
Tunneller biomass	*0.11*	**2.03***	0.61	1.57	1.51	1.39
Dweller richness	*0.61*	**3.49*****	0.15	1.23	0.89	**2.42***
Dweller abundance	*0.20*	1.77	0.53	0.16	0.36	1.91
Dweller biomass	*0.10*	0.29	0.14	0.11	0.26	**2.12***

* $P < 0.05$.
*** $P < 0.001$.

Table 3

Multivariate GLM results for the site ($n = 120$) variables of land use, bait type, mammal richness and relative abundance on dung beetle community assemblage composition. The R^2 value represents variance explained by the explanatory variables.

Factor	Res.df	DF	F-value	P-value
All species ($R^2 = 0.13$)				
Land use	118	1	15.30	<0.001
Bait type	117	1	11.60	0.003
Mammal richness	116	1	13.20	<0.001
Mammal relative abundance	115	1	13.69	0.006
Land use * Bait type	112	3	11.13	0.005
Site	113	2	25.04	0.055
Roller ($R^2 = 0.16$)				
Land use	118	1	4.53	0.086
Bait type	117	1	5.94	0.007
Mammal richness	116	1	6.36	0.006
Mammal relative abundance	115	1	4.53	0.376
Land use * Bait type	112	3	5.75	0.007
Site	113	2	13.52	<0.001
Tunneller ($R^2 = 0.14$)				
Land use	118	1	8.47	<0.001
Bait type	117	1	5.59	0.330
Mammal richness	116	1	8.16	0.007
Mammal relative abundance	115	1	8.45	0.016
Land use * Bait type	112	3	4.09	0.502
Site	113	2	9.39	0.075
Dwellers ($R^2 = 0.17$)				
Land use	118	1	11.56	<0.001
Bait type	117	1	8.51	0.005
Mammal richness	116	1	8.39	0.033
Mammal relative abundance	115	1	9.85	0.002
Land use * Bait type	112	3	8.38	0.005
Site	113	2	19.09	0.017

holotype collected 43 years ago (Ferreira, 1976, 1978). *Epirinus flagellatus* (Fabricius), a species previously thought to be restricted to South Africa and Lesotho (Deschodt et al., 2019) was recorded in Namibia for the first time, some 1000 km from the closest other known locality. Other species whose assessment in Namibia is considered data deficient for Red-Listing (Koch et al., 2000) include *Onitis deceptor* (Peringuey) and *Sarophorus* cf. *angolensis* (Klug) (Frolov, 2004).

3.1. Mammal richness and relative abundance

Twenty-two mammal species were identified at sites based on dung surveys (Appendix D). Sixteen were found at sites in the PAs and mainly included large ungulates as well a few carnivore species (representative of cheetah, leopard and hyena). Eight species were present on farms, consisting mainly of livestock and other domestic species (e.g. goats and sheep). Mammal richness was significantly higher on PAs than on farms ($\chi^2 = 7.59$, $P = 0.006$, $df = 1$, residual $df = 116$), while relative abundance was not ($\chi^2 = 0.92$, P = 0.3.59, $df = 1$, residual $df = 116$).

3.2. Dung beetle richness, abundance and biomass

Significantly more dung beetle species were collected on PAs than on farms (Table 1, Fig. 2, Appendix E). More dung beetle species were attracted to wild dung (wildebeest) than to domestic dung (cattle) in PAs, but this effect disappeared on farms (Table 1, Fig. 2). Tunneller and dweller richness was also significantly higher in PAs, with both rollers and dwellers having more species in PAs using wildebeest dung (Table 2). Roller species richness was positively correlated with mammal species richness (Table 2).

Dung beetle abundance was significantly influenced by land-use alone (Table 1), with highest numbers in the PAs (Fig. 2). This response was driven by the tunneller abundance response, as they were significantly higher on PAs (Table 2, Appendix F). Dung beetle biomass was significantly positively correlated with mammal relative abundance (Table 1, Fig. 2). Yet, both rollers and tunnellers had high biomasses in PAs compared to farms, while dwellers had higher biomasses in PAs when using wildebeest dung (Table 2, Appendix F). Biomass measures were also higher in PAs because larger-bodied species seem to be excluded from farms. For example, some of the largest bodied species collected in the present study such as *Heliocopris andersoni* (average mass: 4392,74 mg) and *Heliocopris atropos* (average mass: 1884,01 mg) were absent from farm sites (Appendix B).

3.3. Dung beetle assemblage composition

Dung beetle assemblage composition was significantly different between farms and PAs, which was driven by the tunneller and dweller assemblages (Table 3). The two different bait types also significantly influenced the overall, roller, and dweller assemblages. All assemblages were significantly influenced by mammal species richness, yet only the overall and dwellers were influenced by mammal abundance (Table 3; Appendix F).

Community assemblage composition was also significantly influenced by the interactive effect of land-use and bait type for the overall, rollers and dweller assemblages (Table 3). Pairwise comparisons showed that overall, all combinations of land use and bait type were significant (Appendix D). Rollers mainly showed differences between bait types, although there was similarity between PA cattle dung and farm wildebeest dung. Whereas dwellers showed a strong affinity for particular land-use irrespective of bait used (Appendix D). The R^2 values for the models were relatively low. Therefore, although the variables included here could account for many of the observed differences in dung beetle diversity metrics, additional factors not accounted for in the models

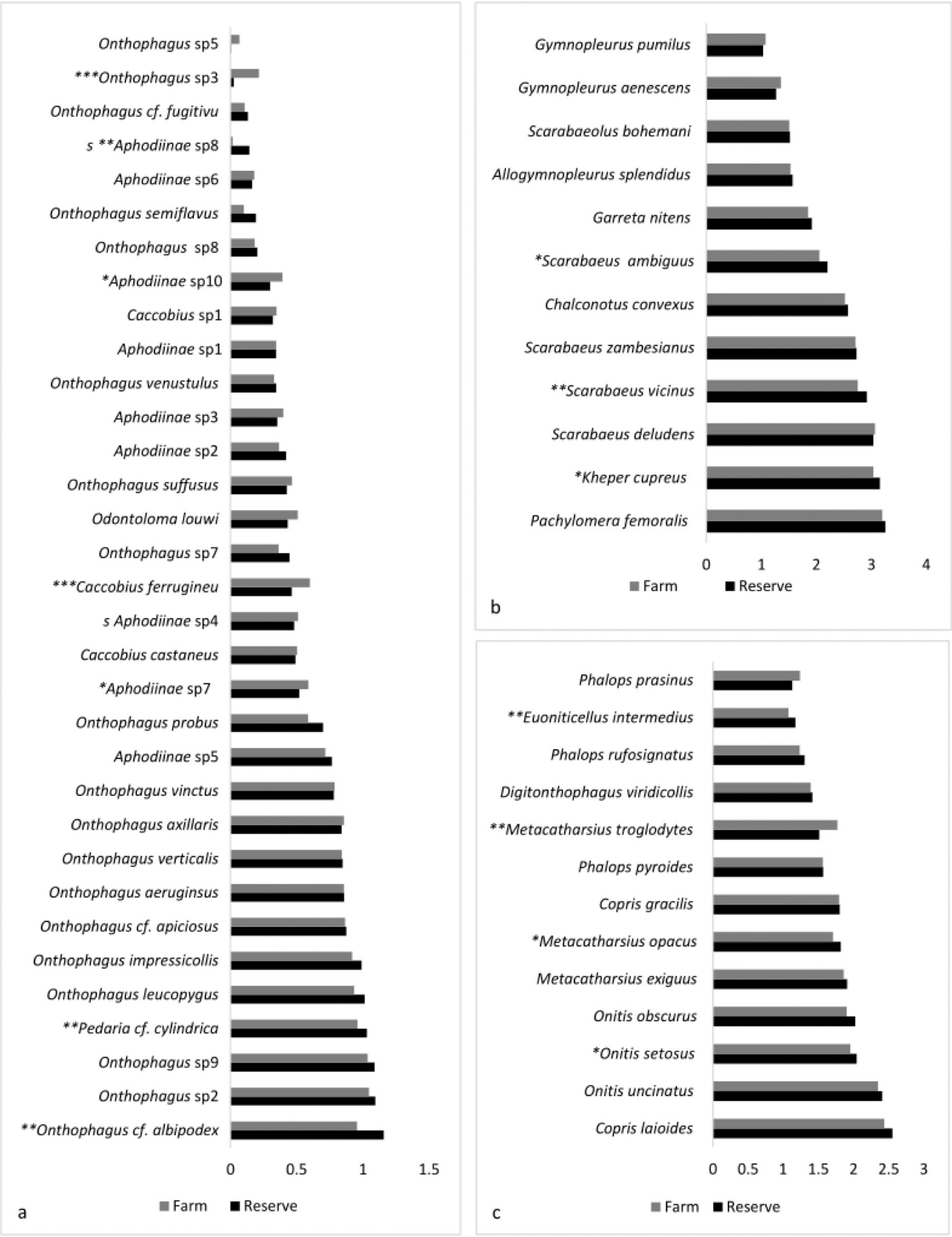

Fig. 3. Bar graphs displaying the mean difference in dung beetle mass on farms (grey) and PAs (black). The x-axis represents the log of the mean mass (mg) of the species and the dung beetle species are listed on the y-axis. Only those species that were present in both farms and PAs are shown here. Grouping of species for bar graphs is according to nesting type: a = dwellers, b = rollers and c = tunnellers. Those species with significant differences are marked with "*" (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

could also influence the response variables (Table 3). There were 17 significant indicator species for PAs (e.g. *Onthophagus* sp8, *Digitonthophagus namaquensis* and *Metacatharsius* cf. *dentinum*) and six indicator species for wildebeest dung (e.g. *Pedaria* cf. *cylindrica* and *Scarabaeolus bohemani*). There were no indicator species for farms and only one species (*Gymnopleurus pumilus*) was an indicator species for cattle dung (Appendix B).

3.4. *Dung beetle body condition*

Overall, individuals of 58 dung beetle species commonly found across both land-uses tended to be larger on PAs than on farms ($G = 12.08$, $P < 0.001$). Only four species were significantly larger on farms (e.g. *Metacatharsius troglodytes* and *Caccobius ferrugineus*) than on PAs, while ten species were significantly larger on PAs (e.g. *Onthophagus* cf. *albipodex* and *Scarabaeus vicinus*) (Appendix B; Fig. 3).

4. Discussion

The most significant variable that influenced dung beetle diversity here, was the comparison between livestock farming and intact natural systems represented by the PAs. This is supported by other studies that cite landscape conversion to agriculture as a major contributor to loss of dung beetle diversity (Jankielsohn et al., 2001; Numa et al., 2012). Reduced mammal richness on farms partially explained reduced dung beetle richness and altered assemblages, as in other systems (Braga et al., 2013; Dangles et al., 2012; Nichols et al., 2009; Raine and Slade, 2019). There were fewer dung specialists, specifically those that prefer native dung on farms (e.g., *Onitis bilobatus* and *Phalops pyroides*) (Du Toit and Cumming, 1999; Tshikae et al., 2008). Livestock behaviour tends to have deleterious effects on vegetation and soil through trampling (Edwards, 1991; Vohland et al., 2005), which will further reduce dung beetle richness (Tonelli et al., 2017).

Abundance was similar on farms and PAs. This was unexpected as insect abundance typically responds negatively to agricultural intensification (Manning et al., 2017), suggesting that cattle may act as surrogates for native mammals and help maintain some ecosystem functioning (Manning and Cutler, 2018). However, biomass was lower on farms due to the exclusion of several large-bodied tunnelling species such as *Catharsius ulysses* and *Heliocopris atropos*, and lower abundance of large rolling species such as *Pachylomera femoralis* and *Scarabaeus goryi*. This is analogous to studies in other systems that documented loss of larger tunnelling and rolling species, due to habitat degradation (Larsen et al., 2008; Dangles et al., 2012). Large species contribute relatively more to ecosystem function, likely leading to an overall reduction of functions and services on farms in the current study (Larsen et al., 2008b; Scholtz et al., 2009; Tonelli et al., 2017).

We show that dung beetles have a greater preference for dung originating from native mammals on PAs, but not on farms and this was evident for richness, abundance and assemblage composition. In PAs, expression of the long evolutionary history that dung beetles and native fauna share was therefore maintained (Nichols et al., 2009; Raine et al., 2018). With the removal of native mammals from agricultural land, a loss of the most specialised dung beetle species leads to the persistence of generalist (euryphagous) taxa. Generalist feeding is often a corollary of resource scarcity (Dormont et al., 2010) and many species in the study region are expected to be generalists as is often the case in arid regions with seasonal fluctuations of migrating mammal populations (Edwards, 1991; Vohland et al., 2005). Dung beetles make choices based on olfactory cues that do not provide any nutritional information (Dormont et al., 2010). Therefore, there is likely some resource conditioning (due to changing dung resources) in some species towards more dominant dung sources in their immediate surrounds (Tshikae et al., 2008; Scholtz et al., 2009).

Contrary to previous studies that only investigated a few species (Schwab et al., 2016; Salomão et al., 2018; Villada-Bedoya et al., 2019), we show a general trend in the mass of dung beetle individuals (58 species), that occur on both farms and PAs tend to be smaller on farms. We believe that this is linked to greater resource quality on PAs than on farms. The average nitrogen content of dung resources on farms is expected to be lower than those on PAs (Augustine, 2003; Codron et al., 2006) and decreased nitrogen content will directly result in the development of smaller-bodied individuals (Edwards, 1991; Schwab et al., 2016). Reductions in quality of dung of domestic livestock may also be due to the use of veterinary medical products excreted with dung (Lumaret et al., 1992; Hammer et al., 2016; Frank et al., 2017). Dung beetles are more vulnerable to veterinary pharmaceuticals under dry conditions, such as in the arid study region here (Scholtz et al., 2009). The negative effects of veterinary medicinal products on dung beetle development are antithetical given that one of the main services provided by dung beetles is the suppression of parasites (Nichols et al., 2008), an action that may be reduced because of its use. Larger individuals are fitter than their smaller counterparts as they are better competitors for food resources and mates (Larsen et al., 2008; Slade et al., 2007; Nervo et al., 2014; Tonelli et al., 2017). Reductions in the average size of individuals of many species on farms may be compromising the ecosystem function provisioned by dung beetles on these farms (Braga et al., 2013; Nervo et al., 2014; Raine et al., 2018).

5. Conclusions

The savannah biome of northern Namibia has proven to be exceptionally rich in dung beetle diversity that exceeds numbers in tropical rainforests and other African regions (Tshikae et al., 2008; Pryke et al., 2016). Richness was higher on PAs, and assemblages differed significantly between farms and PAs, indicating strong negative effects of livestock farming on dung beetle diversity. This emphasises that diverse assemblages of native mammals maintain dung beetle diversity (Pryke et al., 2016; Raine and Slade, 2019; Filazzola et al., 2020). Here we highlighted some of the ways in which land-use change and the replacement of wild mammalian fauna with domestic livestock in Namibia impacts dung beetle abundance, richness, assemblages, overall biomass and body condition, all of which had been affected adversely. The most noteworthy changes detected were the loss in large-bodied species and the difference in the size of the beetle individuals between natural and agroecosystems. These changes may have major short– and long-term implications for the maintenance of important ecosystem processes (Nichols et al., 2009). This underscores the need for a complex amalgam of mammal species to create heterogenous niches, not only for dung beetles but also other invertebrate fauna (Pryke et al., 2016). The preservation of functionally complete dung beetle assemblages is essential to enable continued efficient ecosystem functioning (Manning et al., 2016) and the environmental, agricultural and health advantages they bring (de Klerk, 2004; Beynon et al., 2015).

CRediT authorship contribution statement

Heather U. J. Nependa: Conceptualization, Methodology, Resources, Investigation, Data curation, Funding acquisition, Formal analysis, Writing- Original draft preparation. **James S. Pryke:** Supervision, Methodology, Formal analysis, Writing- Reviewing and Editing, Visualization. **Francois Roets:** Supervision, Conceptualization, Methodology, Writing- Reviewing and Editing, Validation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Christian Deschodt for support in dung beetle identification. Financial support came from Namibia Nature Foundation's Nedbank Go Green Fund. The study was conducted under Permit No. RPIV000142017 provided by the National Commission on Research, Science and Technology in Namibia.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2021.109211.

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