Dung Beetle Diversity and Community Composition Along a Land Use Gradient in a Savannah Ecosystem of North Western Tanzania

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Abstract
Habitat loss and degradation are the most widely cited drivers of changes in species abundance and diversity. We explored changes in dung beetle species diversity and composition across different land uses in the north west Tanzanian savannah. We expected a negative response gradient in the diversity and composition of the dung beetle community, from land uses that preserve vegetation and hold native mammal diversity to livestock intensive and heavily grazed areas. Dung beetles were sampled in a protected area and two anthropogenically influenced land use types. Species richness and composition of each land use type, including differences in diversity and functional groups were analyzed and indicator species for each land use gradient were identified. As expected, diversity and community composition varied between areas with less environmental change compared to those impacted anthropogenically. We conclude that conservation of protected areas within African savannahs can provide a functionally rich dung beetle community and subsequently rich ecological functions. The dung beetle species identified by this study as eco-indicators can be used as a benchmark for future studies that use rapid monitoring to assess disturbance in African savannas.

Information on the distribution of biodiversity is the basis of conservation planning and priority setting (Margules & Pressey, 2000; Wilson, 2000; Wu et al., 2014) and the importance of documenting arthropod species occurrences are never as warranted given the recently documented severe and ongoing declines in insect abundance and diversity (Hallmann et al., 2017; Janzen & Hallwachs, 2019; Sánchez-Bayo & Wyckhuys, 2019). Habitat loss and degradation are the most widely cited drivers of these losses, yet to date most surveys have concentrated on historically industrialised nations and not in the emergent economies of Africa and South East Asia where land use conversion from natural habitats to both subsistence and industrial agriculture is intensifying (Cotula et al., 2009).

Limited resources are available to assess the impacts of land use change on ecosystems, thus financial and time efficient methods such as the use of ecological indicators or 'eco-indicators' have gained recognition in recent years (Gerlach et al., 2013; Lawes et al., 2017). Dung beetles are known to be good indicators of disturbance as they are ubiquitous, diverse, easy to sample, and ecologically important (Davis et al., 2001; Estrada

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& Coates-Estrada, 2002; Spector, 2006). In particular, dung beetles have been proposed as effective indicators to analyse the effects of forest fragmentation (Nichols et al., 2007) and reduced impact logging (França et al., 2017) as well as indicators of tropical forest restoration success (Derhé et al., 2016) and forest type (Stanbrook, Wheater, et al., 2021). However, little research to date has been conducted on the use of dung beetles as indicators of habitat quality in other ecosystems (Carvalho et al., 2020), notably east African grasslands, where increasing agricultural encroachment (Davis, 2002) and commercial livestock grazing (Skarpe, 1991) are driving desertification (Peters et al., 2006).

Alpha diversity and species richness are the most commonly used measurements to evaluate the effects of human disturbance on ecosystems but these metrics assume that all species exert equal influence on ecosystemfunctioning(Barragán et al., 2011). The relationship between these metrics and ecosystem functioning is typically positive as it greater species diversity leads to functionally richer assemblages which can provide multiple ecosystem services (Manning et al., 2016). The evaluation of functional diversity considers the effects that individual species traits have on ecosystems and the impact their removal may have on ecosystem stability. It has been proposed that anthropogenic disturbance may result in the extirpation of species with certain beneficial functional traits which may in turn affect ecosystem functioning (Díaz et al., 2013; Heilpern et al., 2018; Piccini et al., 2018).

Through dung relocation behaviour, dung beetles provide numerous ecological functions including biological pest control, soil fertilization and seed dispersal (Nichols et al., 2007) which contribute to ecosystem service provision. The execution of these functions is positively related to biomass, body size of the organisms (Nervo et al., 2014; Stanbrook, Harris, et al., 2021), and the complementarity of species and functional guilds (Slade et al., 2007). In particular Slade et al. found that tunnellers, especially nocturnal tunnellers, played a larger role in dung removal compared to rollers; tunnellers alone removed approximately 50% of dung, while rollers alone removed approximately 30% of the dung mass. Tunnelers were also responsible for removing twice the amount of dung compared to rollers in forested sites in Brazil (Batilani-Filho & Hernandez, 2017). Multiple lines of evidence indicate that local and regional scale changes in land use can severely alter patterns of dung beetle species diversity and abundance (Bogoni et al., 2016; Culot et al., 2013) and the decline of dung beetle fauna will impart long term implications on the maintenance of ecosystem integrity (Manning et al., 2016; Nichols et al., 2008).

To investigate the effects of land management intensity on dung beetle communities, we assessed the diversity of dung beetles along a disturbance gradient: a Game Controlled Area (GCA), a pastoral area, and a community area where a mixture of pastoralism, settlements and small holder farming are the main land-uses. This study describes changes in dung beetle communitiy composition across a land use gradient and we believe is one of the first to document the impact of anthropic pressures on East African dung beetle communitities. We predicted that dung beetle richness and diversity would be higher inside the protected and pastoral areas and lowest in the community area. This study aims to describe the dung beetle diversity and functional diversity that are present within each land use type and analyse their potential ecological role. Additionally, we indentified which species could be considered ecological indicators for each land use gradient.

Methods

Description of the Study Area

All three study sites were located in the Kwakuchinja wildlife corridor between Lake Manyara National Parks and Tarangire National Parks in Northern central Tanzania (Figure 1). This corridor is part of Kwakuchinja Open Area which covers about $600\,km^2$, bounded by parallels 03° 35′ 38″ and 03° 48′ 02″S and meridians 35,048′ 21″ and 35° 59′ 25″ E (Martin et al., 2019) and forms part of the Tarangire - Manyara ecosystem (TME) which has high mammal species diversity (Pittiglio et al., 2012). The corridor was classified as 'critical' by Caro et al. (2009) who noted that the high density of human settlements and expansion of croplands were threats affecting the corridors future existence. The vegetation type is primarily microphyllous savannah dominated by *Acacia tortillis* and interspersed with *Commiphora* woodland. Rainfall is characteristically bimodal with short rains from November to January and long rains from February to May. The average rainfall is 600–650 mm *per annum* (Galanti et al., 2006)

Kwakuchinja is used by pastoralists as a transit corridor for goats and cattle between water sources and is greatly impacted by livestock overgrazing and daily fire wood collection. It is located adjacent to Mdori village (3⁰47'30" S, 35,056' 55" E) within an area owned by the College of African Wildlife Management. Vegetation is heterogeneous, with *Acacia* savannah occurring alongside broadleaf deciduous vegetation around recently established water holes. Human population density is estimated to be 100 – 200 people per km^2 (Caro et al., 2009). The study site suffers from a paucity in wild mammal species and is dominated by domestic goats and cattle.

Minjingu village is located adjacent to Tarangire National Park (3⁰46'19" S, 35⁰51'29" E). The area
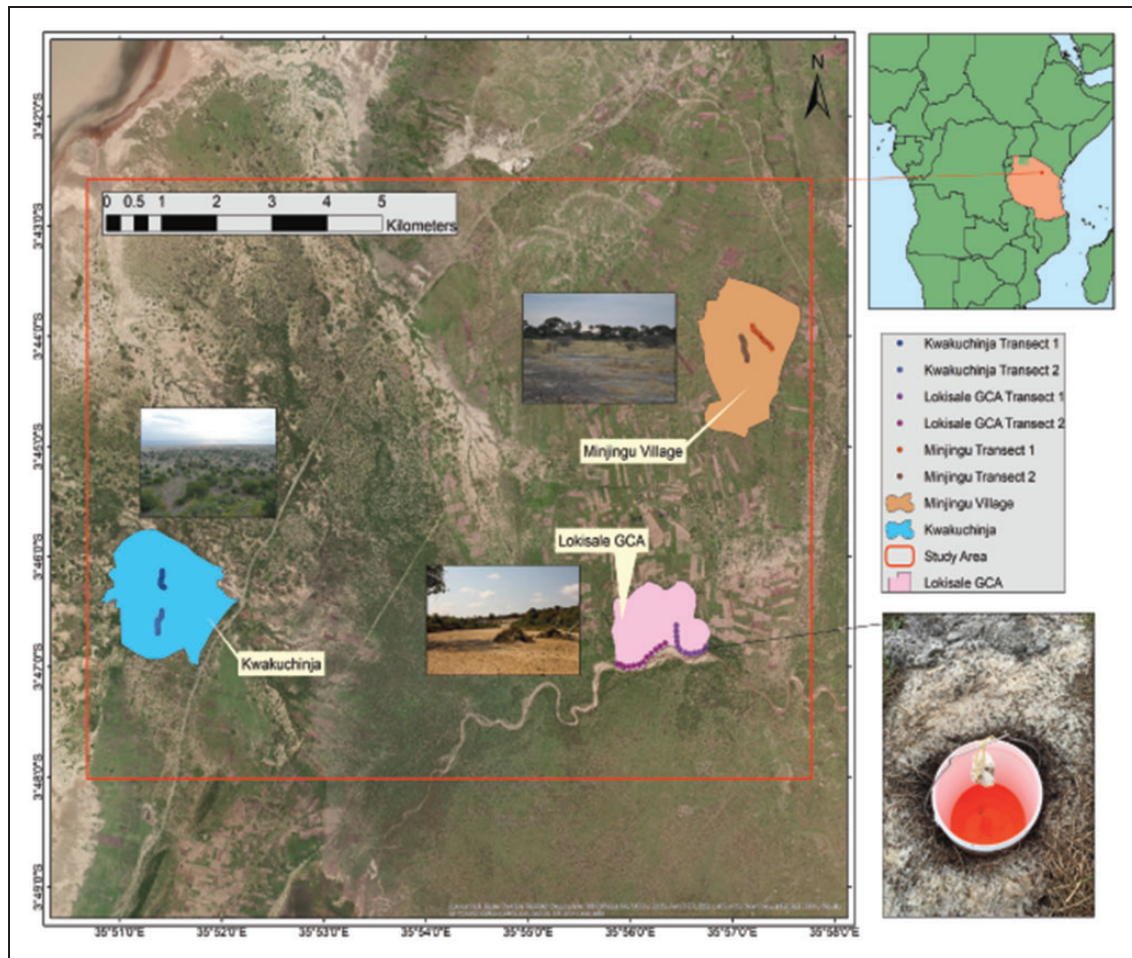
Figure 1. Map of Study Locations.

suffers from overgrazing by livestock and there are many agricultural small holdings. The vegetation is dominated by *Acacia tortilis* and *Balanites aegyptiaca*, and by invasive and pioneer species *Solanum incanum* and *Alternanthera pungens*. A variety of mammals including elephant (*Loxodonta africana*), wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*) are present.

The Lolkisale Game Controlled Area (GCA) (3^0 46' 10" S, $35^0$57'30" E) is a protected area covering $15 \, km^2$ and is also adjacent to Tarangire National Park (TNP). It was gazetted 1974 and categorised as a protected area with sustainable use of natural resources including hunting (Despot Belmonte & Bieberstein, 2016) by the IUCN. Game Controlled Areas (GCA's) are type of protected area provided for in Tanzania's Wildlife Conservation Act of 1974. In accordance with the Act, human settlement and the grazing of livestock are unrestricted, and hunting of wildlife is only permitted under licence (Weldemichel, 2020). Twenty-five large mammal species have been recorded within GCA (Martin et al., 2019) including high abundance of game species including zebra (*Hippotigris quagga*), Grants gazelle (*Nanger

granti*), impala, (*Aepyceros melampus*) , Hartebeest (*Alcelaphus buselaphus*) and Buffalo (*Syncerus caffer*). These mammals provide rich and varied dung resources that are expected within savannah regions and required for supporting robust and diverse dung beetle assemblages.Hanski and Cambefort (1991) found that beetle (species) size is strongly influenced by mammal composition, as well as spatial proximity, and other studies have found there is a greater proportion of small-bodied beetles in situations where large mammals are absent (Nichols et al., 2013). There is no fence between the TNP and the GCA allowing the free movement of animals between the two protected areas. Vegetation is primarily *Commiphora–Combretum* deciduous woodlands.

Trapping Methods

Sampling was carried out between 18 June - 10 August 2013. Twelve pitfall traps *per* study site were placed 50 m apart on a linear transect in accordance with (Larsen et al., 2005). Each site contained two transects of six

traps (Figure 1) and trapping was conducted for four consecutive days per transect to provide a trapping effort of eight days *per* site. Each pitfall trap comprised a 1 litre plastic tub sunk into the substrate up to its rim and filled with a saltwater and soap solution. Traps were baited with 40 g of fresh pig dung wrapped in fine gauge mesh netting which allowed dung volatiles to be emitted while excluding dung beetles. The bait was supported above each trap by a tripod of stakes and secured by string. Traps were emptied and re-baited every 24 hours to provide a total sample of 96 samples per site and total of 288 collections for study. Once collected, the dung beetles were transferred into a 70% ethanol for preservation and identification. Preserved specimens form part of a vouchered reference collection housed at the Oxford University Museum of Natural History (OUMNH).

Dung Beetle Identification

We identified the species of Scarabaeidae using taxonomic keys (D'Orbigny, 1913; Ferreira, 1969) unpublished species lists, and collections of the Oxford University Museum of Natural History Museum (OUMNH), with assistance of Darren Mann from OUMNH. Where specific identification was not possible, specimens were identified to genus and then assigned to a morphospecies. The community structure was categorised using the functional classification of African Scarabaeine dung beetle groups proposed by Doube (1990) (see Supplementary Table 1). Functional group classification sensu Doube (1990) provides a simple guideline for determing the structure of diverse assemblages of African dung beetles in a way that reflects a species functional role within a habitat. The classification is primarily based on the ways in which dung beetles compete for, use, and disrupt dung.

Environmental Data

Tree canopy cover above each of the 72 traps was measured using a spherical densiometer and expressed as a percentage of total leaf cover. Ground cover (%) was measured using one 1 m^2 quadrat placed at random within a 20 m radius of each pit fall trap. The percentage of bare ground was calculated by recording the presence or absence of bare ground at 50 cm intervals along a 10 m transect perpendicular to the pitfall trap. Data on classified landcover type was extracted from 30 m resolution landcover maps from 2010 (https://rcmrd.africageoportal.com) for each study location. The distance to the nearest water body was ascertained using nearest neighbour analysis in QGIS 3.10.11 for each pitfall trap. Water body data included lake and river data for Tanzania and was obtained from worldbank.org. Additionally, digital elevation data at 30 m resolution

was extracted for each pitfall trap location and was obtained from SRTM (Shuttle Radar Topography Mission) using data available from usgs.gov.

Data Analysis

Rank abundance curves (RAC) were constructed using the R package 'BiodiversityR' (Kindt & Coe, 2005) to assess abundance and species dominance in each study site. A Shapiro-Wilks test was used to ascertain normality, all variables were found to be normally distributed. We evaluated the changes in mean species richness, diversity, and abundance of dung beetle between locations using generalized linear mixed models (GLMMs). To control for spatial autocorreltion in these models, Management was considered as a fixed factor and transect as a random factor. For species richness and abundance data, a Poisson distribution was assumed (count data) and for species diversity a gamma distribution was used. GLMMs were conducted with the nlme package (Pinheiro et al., 2017). Tukeys post-hoc pairwise comparisons were then used to describe compare differences between species richness, abundance and management using the glht function found in the package 'multcomp' (Hothorn et al., 2008) Alpha diversity measurements were calculated for each site using Shannon–Weiner, Simpsons and Berger-Parker indices. The Shannon-Weiner index places greater weight on the addition of new species regardless of rarity while Simpson's index is biased towards the more abundant species within a sample (Magurran, 2004). Thus, both indices were used for comparative purposes to describe the alpha diversity of each site.

The Berger-Parker dominance index was calculated using the package 'BiodiversityR' version 2.10.0. The index is calculated by dividing the number of individuals in the most abundant species by the total number of specimens present in the sample (Berger & Parker, 1970). An increase in the test statistic d equates to a decrease in diversity and an increase in species dominance in the sample. It is therefore a useful measure to deduce which sites contain species with a large impact on community structure (Morris et al., 2014) and the resultant diversity of the habitat. Chao1 (Chao, 1984) was used as a species richness estimator to calculate the expected species richness for each site. Richness estimations were then used to compare sampling efficiency.

Kruskal-Wallis with Dunns post-hoc tests were used to assess differences in elevation, distance to the nearest permanent water body, amount of bare ground, and ground and canopy cover for each study location. As sites nearby each other may naturally have more closely related biological communities than those further apart (Soininen et al., 2007), we checked for spatial autocorrelation by performing Moran' s I tests (Moran, 1950)

using both dung beetle species richness and abundance data, at trap and transect levels allowing us to examine whether spatial auto-correlation existed in both sets of analysis.

A Non-Metric Multidimensional Scaling (NMDS) analysis using species level abundance data with a Bray-Curtis dissimilarity index was calculated to look at the community composition of dung beetle species between land uses using the R package 'vegan' (Oksanen et al., 2013). We then examined the effects of percent canopy cover, percent ground cover, amount of bare ground elevation and distance to permanent water source on community composition with PERMANOVA on Bray-Curtis distances calculated from species abundances with 999 permutations, using the adonis function in the vegan package. Because PERMANOVA and NMDS cannot readily account for spatial autocorrelation, spatial effects were not included in these analyses of cumulative patterns. A Chi squared test of association was used to look for a relationship between dung beetle functional groups and land use type. All analyses were carried out in the software programme R v3.5 (R Development Core Team, 2019).

IndVal

The IndVal method (Dufrene & Legendre, 1997) was used to determine characteristic species for each land use type. Most ecological and environmental bio indicators are identified by establishing a strong relationship with some characteristic of their environment. The IndVal method reflects frequency of occurrence (abundance) of species between habitats and is calculated by comparing a species' frequency of occurrence between habitat types (Mcgeoch, 2007). Species with high IndVals (>70%) thus make reliable indicator species not only because they are specific to a locality, but also because they have a high probability of being sampled in that locality during monitoring and assessment (McGeoch et al., 2002). Species were categorised as an indicator of a particular habitat if the IndVal measurement for habitat fidelity was >70%. Those species with an IndVal measurement between 20–50% were classified as generalists.

Results

Environmental Parameters

Elevation (m asl) was found to be statistically different between study locations (Kruskal–Wallis, $X^2 = 34.00$, $P = <0.05$, df = 2). Median elevation was found to be greater in Minjingu with a median elevation 1005 m compared to 986 m in Kwakuchinja and 998 m in Lokisale GCA. Distance to the nearest permanent water body was also found to be different between locations ($X^2 = 63.12$, $P = <0.05$, df = 2) with the median distance varying from 11.76 Km in Kwakuchinja to 7.08 km in Minjingu, and 2.79 km in Lokisale. Vegetation also differed between the three study locations. Canopy cover was significantly different between sites (Kruskal–Wallis, $X^2 = 18.76$, $P = <0.05$, df = 2) with Minjingu having significantly less coverage compared to Kwakuchinja and Lokisale GCA (Figure 2). There was no significant difference in the amount of ground cover between study locations.

Variation in Dung Beetle Assemblages Between Land Use Type

Species Richness and Diversity. A total of 1371 individual of 45 species and morphospecies belonging to 8 tribes (*Onthophagini, Canthonini, Coprini, Sisyphini, Scarabaeini, Gymnopleurini, Oniti, Oniticellini*) were recorded over the study period of 24 trapping days. The number of individuals collected in the three environments differed significantly (one-way ANOVA, F = 4.7, d.f = 69, p < 0.01). The Kwakuchinja site had the greatest abundance of beetles with 608 individuals representing 44.4% of the total followed by; Lolkisale GCA with 509 individuals (37.1%) and the Minjingu site 254 individuals (18.5%).

Species richness also differed by land use type, with Lolkisale GCA the most speciose with 21 species (44.6%) followed by Kwakuchinja (17; 36.17%) and Minjingu village (12; 25.53%) (Table 1). The most abundant species overall were, *Onthophagus* sp. 14, *Onthophagus* sp. 2, Digitonthophagus *gazella*, *Sisyphus* sp 1, and *Caccobius sp 1* with 283 (20.6%), 214 (15.6%), 133 (9.7%) and the two latter ones with 118 (8.6%) and 57 (4.15%) individuals each. These five species accounted for 63% of all individuals collected, demonstrating that all sites were dominated by a few abundant species and fit a geometric series distribution. The protected area at Lolkisale GCA was the only site to reach an asymptote of species richness (Figure 3). Using Chao 1 as a population estimator it was calculated that 85.7% of the true species richness was collected across all three sites (Table 1).

Shannon-Weiner, Simpsons and Inverse Simpsons indices were calculated for each site (Table 1). The results of the Shannon-Weiner diversity index indicate that of the three sites sampled Lolkisale was the most diverse (H'=2.579) followed by Minjingu (H'=1.827) and Kwachuchinja (H'=0.757). The Simpsons Diversity index resulted in identical evenness and species richness between the Kwachuchinja and Lolkisale (0.979). The results of the inverse Simpsons index indicate little difference in species dominance between Kwachuchinja and the Lolkisale Game Controlled

Table 1. Species Richness and Diversity Indices for each land use type, Lokisale Game Controlled Area (GCA), Kwakuchinja (KWA) and Minjingu (MIN).

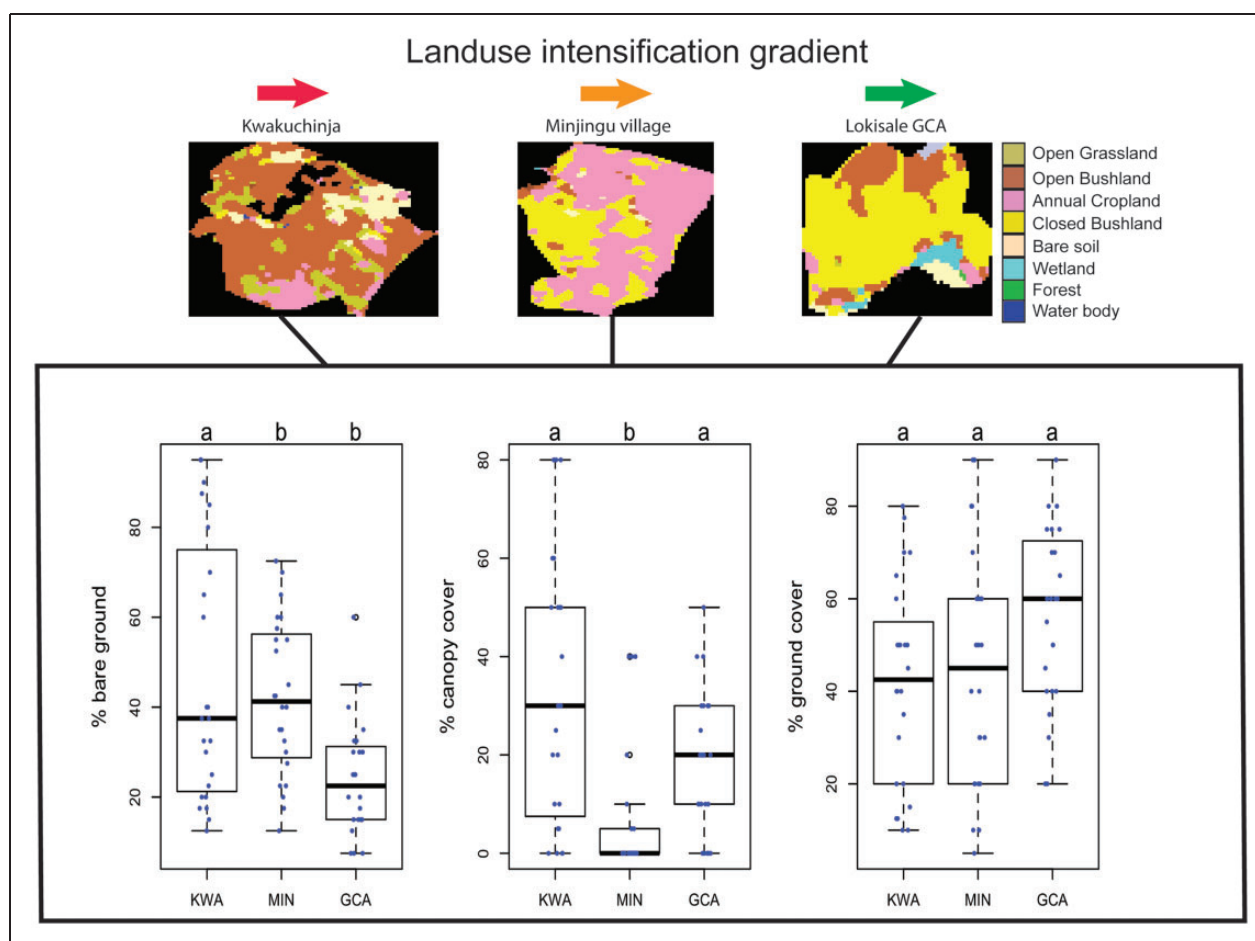| Site	Species richness (s)	Abundance (n)	Shannon ('H)	Simpson ('D)	Berger-Parker	Chao1
Kwakuchinja	17	608	1.8	0.73	0.47	17
Minjingu village	12	254	0.76	0.29	0.84	14
Lokisale GCA	21	509	2.6	0.89	0.23	21

Figure 2. Percent Cover of Bare Ground, Canopy Cover and Ground Cover Between Land Use Type, Lokisale Game Controlled Area (GCA), Kwakuchinja (KWA) and Minjingu (MIN) (Median, Interquartile Range and Whiskers and Outliers). Different letters indicate significant differences with $p < 0.05$. Landcover map generated from 30 m resolution Landsat 7 data.

Area (GCA) but due to the greater dominance of *Onthophagus* sp2 at the Minjingu site, the distribution had a steeper slope (Rank abundance curves *per* site shown in Figure 3). The species abundance distribution was calculated using the Berger-Parker index (Berger & Parker, 1970). The results of the index demonstrated decreased diversity in the Minjingu site because of the greater dominance of *Onthophagus* sp2 (84.2%) when compared to that of the dominant species found in the other study sites (Table 1): *Onthophagus* 14 (20.6%) and *Sisysphus crispatus* (23.2%).

NMDS ordination of sampling units based on similarity of species abundance resulted two consistent and segregated groups as follows: (a) one formed by the degraded Kwakuchinja site and (b) two overlapping groups formed by the moderately disturbed Minjingu sites and another overlapping group formed by sites in the GCA (Figure 4). This clear segregation, particularly in terms of degraded vs. less disturbed were supported by ANOSIM tests, which detected a strong effect of landuse type ($R = 0.830$, $p < 0.001$). PERMANOVA indicated that canopy cover, amount of bare ground, study location and elevation all
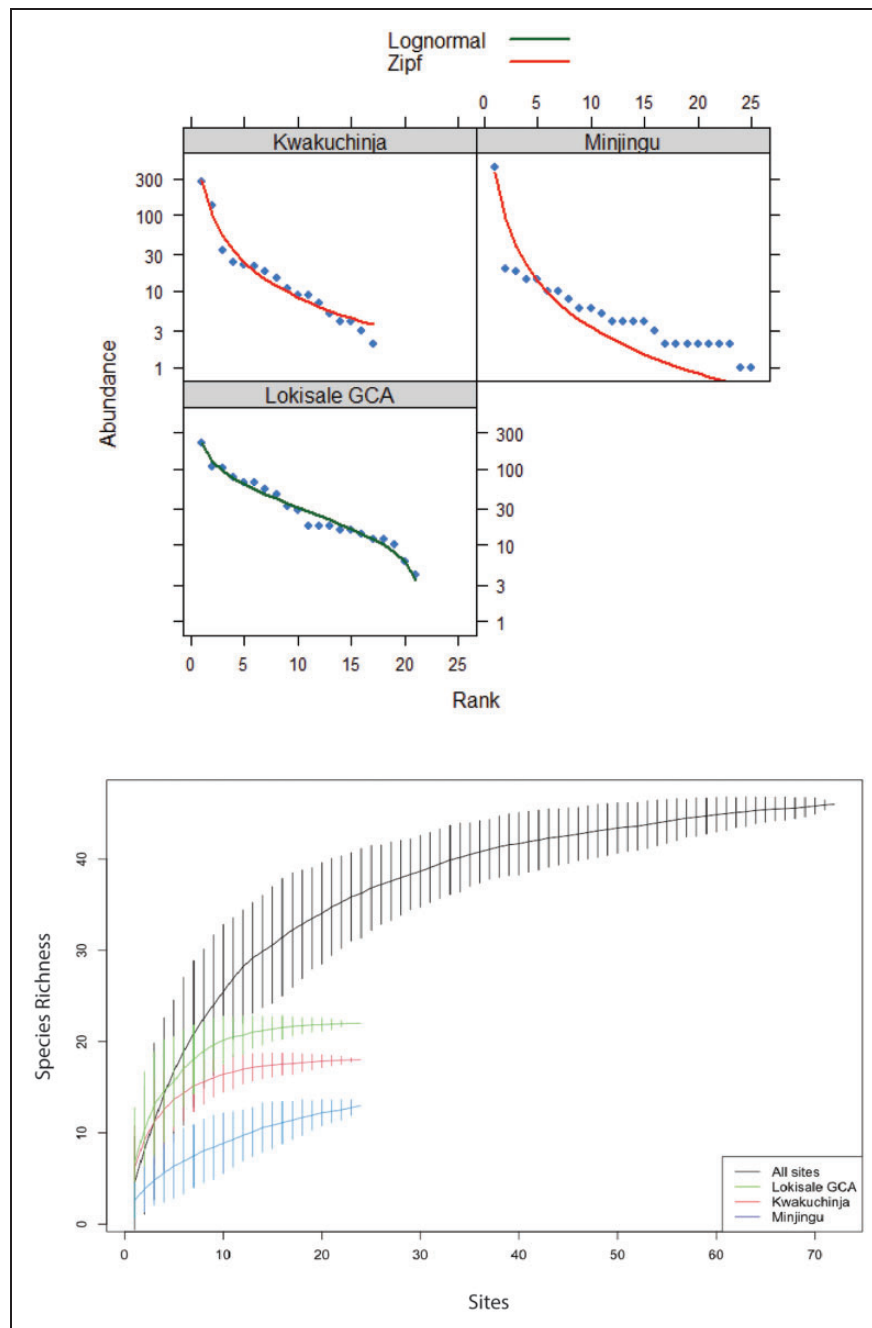
Figure 3. Rank abundance and species accumulation curves for each land use type in order of land use degradation: Kwakuchinja (KWA) and Minjingu (MIN) and Lokisale Game Controlled Area (GCA)..

had significant effects on community composition (Table 2). The clustering and overlapping of the Minjingu and Lokisale sites is reflective of how strongly habitat characteristics may shape dung beetle community compositions over an acute spatial scale. Species composition in traps located in Kwakachinja sites had little compositional overlap with any of the Minjingu or Lokisale sites, and half of the traps located at the moderately disturbed

Minjingu site comprised a mixture of species compositions from both the protected Lokisale GCA study site and the domestic livestock abundant Kwakachinja site. Three trapping locations in Minjingu were ordinated outside of the main cluster. This is likely due to a lower abundance of individuals per trap with (2,7, and 5 individuals respectively) and were traps dominated by a single species of Onthophagine.
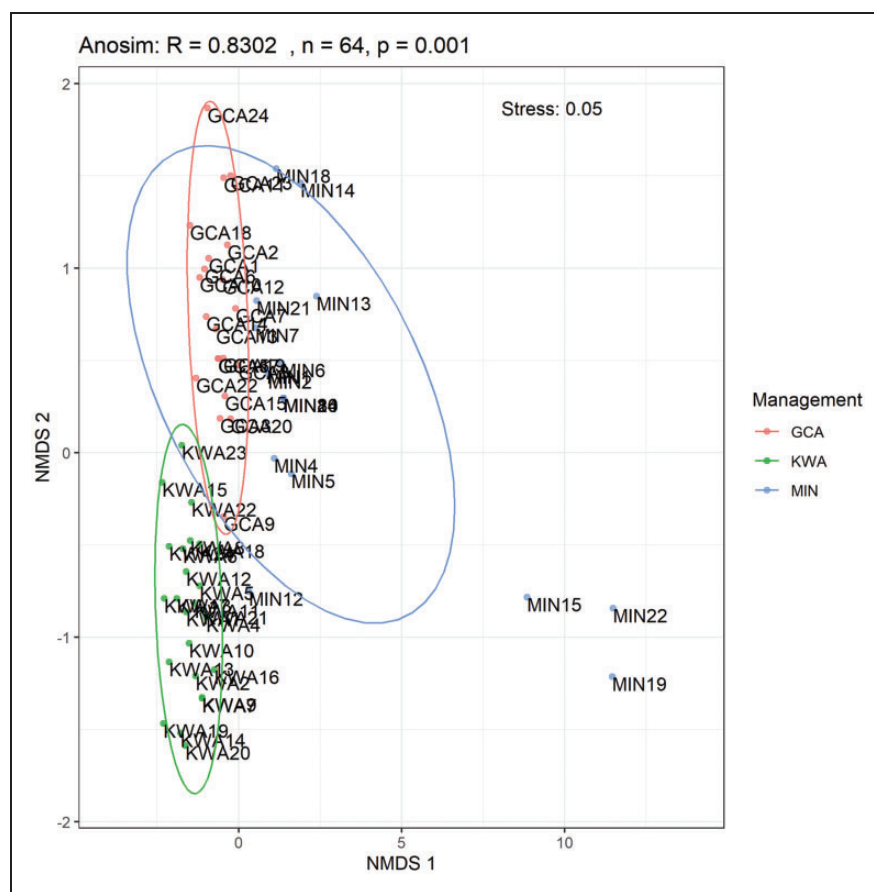
Figure 4. NMDS Plot Based on Dung Beetle Community Composition Between Three Land Use Types Along a Land Use Gradient in a Savannah Ecosystem of North Western Tanzania. In order of land use degradation: Kwakuchinja (KWA), Minjingu (MIN), Lokisale Game Controlled Area. NMDS based on abundance data using Bray Curtis dissimilarity index.

Table 2. Environmental Variables Analysed by PERMANOVA using Adonis. Bolded text denotes statistical significance at $p < 0.05$.

Predictors	F (df)	R^2	P value
Canopy cover	6.87 (1,63)	0.07	**0.001**
Ground cover	1.82 (1,63)	0.01	**0.048**
Bare ground	1.97 (1,63)	0.02	**0.033**
Management	12.76 (2,63)	0.26	**0.001**
Elevation	1.76 (1,63)	0.01	**0.048**
Distance to H_2O	1.3 (1,63)	0.01	0.187

Analysis of Functional Groups

All individuals were assigned to functional groups based on their dung relocation strategy and body size. The most abundant functional group was Group V containing the small-medium paracoprid, coprophagous species (Doube, 1990). The least abundant functional group was Functional Group VII small, diurnal, coprophagous, endocoprids. In all the sites, Functional Group V (hereafter F.G V) was most dominant comprising 41.17%, 49.98% and 23.80% of the total number of individuals

respectively (Figure 5). Lolkisale Game Controlled Area (GCA) was the only site that had all seven functional groups represented and also contained the greatest overall species diversity (Table 1). All individuals identified as F.G VII were trapped in Lolkisale Game Controlled Area (GCA) demonstrating that smaller dweller species preferred conditions with increased vegetative cover and varied dung resources. Beetles belonging to FGII, the small telecoprids were entirely absent from the disturbed Minjingu site.

Dung Beetle Species as Indicators of Habitat Quality

The indicator value (IndVal) method (Dufrene & Legendre, 1997) combines measures of habitat fidelity and specificity was used to ascertain which species could be used as indicators of biological change within each study site. A total of 17 species trapped in all study sites could be considered 'indicator species' (McGeoch et al., 2002) (Table 3). *Gymnopleurus sericeifrons* trapped in Lolkisale Game Controlled Area (GCA) had the highest %IndVal of all species collected (97%) and can be
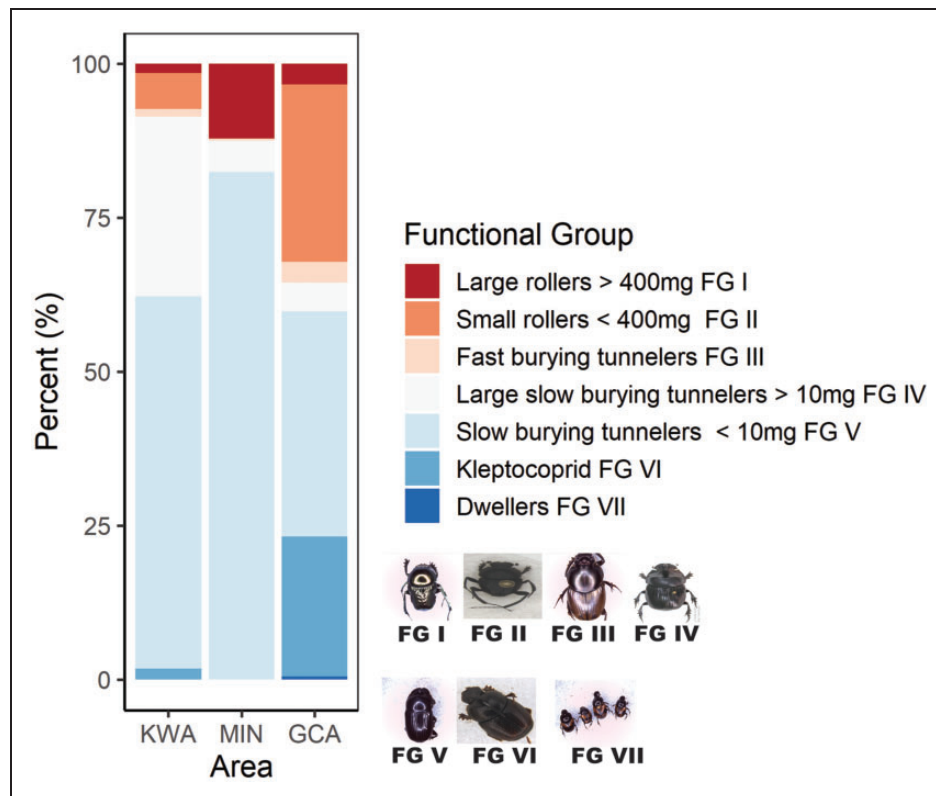
Figure 5. Percentage of Each Functional Group Found in Each Land Use Type. Landuse degradation gradient: Kwakuchinja (KWA) -> Minjingu (MIN) -> Lokisale Game Controlled Area.

considered a species characteristic of the site. Lolkisale Game Controlled Area (GCA) had a larger complement of more characteristic dung beetle species than both Kwachchinja and the Minjingu site. *Onthophagus* sp13 returned the highest IndVal for the Minjingu site (94%) but could not be a considered a reliable indicator of the habitat condition of the Kwachuchinja site as it represented a < 70% IndVal. Both species in the genus *Sisyphus*; a small, diurnal, telecoprid trapped in the Lolkisale Game Controlled Area (GCA) had >70% indicator values signifying that this habitat is favourable to species that require increased vegetative cover.

Discussion

Abundance and Diversity

Overall we found; (i) a difference in the abundance of dung beetles between non-protected and protected sites (ii) the livestock rich kwakachinja contained the highest abundance, and the moderately disturbed site at Minjingu which contained a mixture of livestock and wildlife contained the least (iii) dung beetle diversity was higher in the protected land use site compared with the unprotected sites and, (iv) dung beetle functional composition changed concomitantly with land use type. Our hypothesis that a reduction in the vegetative heterogeneity in the disturbed sites would also reduce the species diversity and abundance of dung beetles, causing important changes in species assemblage structure was supported. It is known that dung beetle communities display graded responses to a variety of ecological factors and anthropogenic disturbances including ivermectin use (Krüger & Scholtz, 1998), habitat modification (França et al., 2017), habitat fragmentation (Da Silva & Hernández, 2014), vegetation type (Escobar & Davis, 2010) and dung availability (Raine & Slade, 2019) and this may explain the changes in dung beetle diversity we observed.

The Kwachuchinja site possessed the highest percentage of bare ground and the lowest per cent of ground cover due to excessive grazing but also contained the greatest abundance of dung beetles (608 individuals). According to Jankielsohn et al. (2001), high concentrations of domestic livestock within a concentrated area alter vegetation and soil characteristics by overgrazing and causing soil induration. However, a consequence of the high concentration of livestock is increased dung resource availability which results in closer spatial aggregations of dung and reducing the temporal variation of food availability. The findings of the current study are consistent with those of Verdu et al. (2007), Davis et al.

Table 3. The IndVal Values of the Significant Characteristic Species for Each Land Use Type, Lokisale Game Controlled Area (GCA), Kwakuchinja (KWA) and Minjingu (MIN).

Kwakuchinja			Minjingu Village			Lokisale GCA		
Species	IndVal	P	Species	IndVal	P	Species	IndVal	P
Onthophagus sp14	0.87	0.001	Onthophagus sp13	0.94	0.001	*Gymnopleurus sericeifrons*	0.97	0.001
Digitonthophagus gazella	0.66	0.001	*Sisyphus crispatus*	0.79	0.001	Sisyphus (aff. costatus)	0.79	0.001
Onthophagus sp8	0.54	0.001	*Cleptocaccobius convexus*	0.43	0.001	*Sisyphus crispatus*	0.73	0.001
Tiniocellus spinipes	0.41	0.001	Onthophagus sp11	0.41	0.001	Onthophagus sp2	0.62	0.001
Onthophagus sp13	0.29	0.001	Caccobius sp1	0.41	0.001			
Anachalcos convexus	0.29	0.001	Onthophagus sp12	0.37	0.001			
Onthophagus sp9	0.25	0.002	*Khepher aegyptiorum*	0.31	0.002			
Sisyphus (aff. costatus)	0.23	0.031	Onthophagus sp10	0.29	0.002			
Onthophagus vinctus	0.20	0.01	Onthophagus sp7	0.29	0.001			
Onthophagus nigriventris	0.16	0.039	Onthophagus sp9	0.20	0.006			
			Onitis alexis	0.20	0.008			

(2002) and Simelane (2010) who also found that cattle grazing increased dung beetle abundance.

However, both Estrada et al. (1998) and Raine and Slade (2019) note that a large and diverse mammal fauna is also crucial for the maintenance of dung beetle diversity. Lolkisale Game Controlled Area (GCA), contains the highest mammalian diversity and contained megafauna including elephant (*Loxodonta africana*), along with a wide variety of other herbivores such as zebra (*Equus burchelli*), and bushpig (*Potamochoerus larvatus*). This diversity may promote the co-existence of different species of dung beetles, and both generalist and specialist feeders. The data from both the Kwachuchinja and the Minjingu sites followed a geometric series distribution with both sites dominated by many individuals of a single species. The geometric series is typical of disturbed habitats and describes uneven species abundance, low diversity, and communities dominated by a few species (He & Tang, 2008).

Species dominance patterns were similar in both unprotected habitats, with two or three very dominant species in each site, although different species were dominant in the Kwachachinja compared with the Minjingu village sites. *Onthophagus* sp14 was the dominant species representing 20.6% of the total capture in disturbed, livestock dominated Kwakachinja site, *Onthophagus* 2 represented 84.3% of the total capture in the Minjingu site while *Sisyphus* aff. costatus was the most dominant species in the protected Lokisale site.

Jankielsohn et al. (2001) suggests that the abundance, size and ecological role of the dominant species and not just species richness are important factors to consider when assessing the level of disturbance within habitats as not all dung beetles exert the same functionality in the habitats in which they live. Both *Onthophagus* species found in the disturbed sites are small paracoprids which are often comparatively slow at removing dung from the environment (Simmons & Ridsdill-Smith, 2011). As a result, rates of dung degradation can be reduced, and the important ecosystem services associated with dung beetle fauna can be less obviously effective in habitats dominated by smaller weaker species than those dominated by more effective dung degraders. *Sisyphus* 1, the most dominant species in the protected area is a diurnal, medium telecoprid. Sisyphini are highly effective competitors for dung and are able to remove dung quickly from pats and then bury it in short tunnels beneath the substrate (Tshikae et al., 2008).

Community Structure

Functional groups were not evenly distributed across all habitats as some groups were entirely absent from the disturbed Kwakuchinja and Minjingu study sites and others showed strong preference towards the Lokisale site. Functional group 5 (FGV), the smaller slow-burying paracoprids showed the greatest equitability across all three study sites in terms of abundance. This result is in accordance with those of Davis (1996a) who reported a similar abundance of FGV in habitats dominated by Acacia-Commiphora vegetation on sand substrate. The small telecopied species (*Sisyphus*, *Gymnopleurus*) belonging to FGII were entirely absent from the anthropogenically affected Minjingu site. Jankielsohn et al. (2001) noted that the decreases in grass cover and increases in woody shrub cover found in overgrazed habitats may impede the rolling activity of small telecoprids and decrease their ability to detect dung due to odour attenuation. This may explain the absence of the functional group from the study site.

The low percentage of abundance in FGI: the large tele-coprids (*Anachalcos, Khepher, Scarabaeus*) from the Kwakachinja site is perhaps indicative of the paucity of large herbivorous mammals, other than cattle in the area, and reflects the subsequent lack of appropriate dung resources.

A large and growing body of literature has investigated the effects of declining mammal populations and the replacement of native fauna with livestock on dung beetle communities (Andresen, 1999; Culot et al., 2013; Nichols et al., 2009). Slade et al. (2007) note that the largest beetles belonging to FGI remove a disproportionate amount of dung and their decline and eventual extirpation from disturbed habitats could have profound implications for the maintenance of key ecosystem functions such as dung removal. Slade et al. (2016) describe how when this group is absent from tropical forests a 75% reduction in dung removal from surfaces is observed. The FGVII were found exclusively within the protected Lolkisale Game Controlled Area (GCA) and represented just 7% of the total of all individuals caught. Endocoprids breed within dung pats and are the least effective competitors for dung compared other functional groups (Doube, 1990) and therefore offer little towards the maintenance of ecosystem services (Jankielsohn et al., 2001).

Dung Beetles as Indicators of Ecological Disturbance

This study identified 17 species of dung beetle which can be used to ascertain the direction of ecological change with habitats and be used as an indicator of the ecological integrity of each site (Table 3). The majority of indicator species belonged to two functional groups. FGI (large telecoprids), *Scarabaeus* 1, *Scarabaeus* 2, *Scarabaeus* 3, *Kheper aegyptorium*, *Anachalcos convexus* and FGIII (large paracoprids) *Copris* 1, *Copris* 2, *Copris elphenor*. Our results are consistent with those of Jankielsohn et al. (2001) who suggested that modifications in ground cover caused by overgrazing and trampling has a greater effect on the larger bodied species in dung beetle assemblages, while smaller bodied and those species who are less competitive for dung resources not affected to the same degree. Other studies have also found large species of dung beetle have been shown to be more sensitive to ecosystem disturbance (Nichols et al., 2009) and have shown greater susceptibility to abundance decline in anthropogenically modified habitats (Gardner et al., 2007).

In the Lolkisale Game Controlled Area (GCA) three of the species defined as being indicators (*Sisyphus aff. costatus, Sisyphus crispatus, Gymnopleurus serceifrons*) belonged to FGII: small, telecoprids whose dung exploitation behaviour requires both sexes to construct and roll a portion of dung away from a dung source and bury it in a tunnel located some distance from the dropping. This exploitation behaviour requires vegetation cover to be patchy so as not to obstruct rolling behaviour and a solid substrate texture. In his study of differences in African dung beetle communities between habitats (Davis, 1996a) proposes that FGII association is most likely to be found in areas comprising of thicketed vegetation and clay substrate due to the hardness of clay limiting breeding space under dung pats. *Digitonthophagus gazella* returned the highest indicator value for the Kwakachinja site. *Digitonthophagus gazella* is the most widespread dung beetle in tropical and subtropical cattle pastures in the world (Génier & Davis, 2017) and has a natural geographical range of approximately 15million Km^2 (Scholtz et al., 2009). One of the more significant findings to emerge from this study is the discovery of a single *Euoniticellus parvus* during sampling at the Lokisale study site. The species was thought to be endemic to western Africa: Cote d'Ivoire, Gambia, Sierra Leone (Ferreira, 1972) but was first discovered in eastern Africa inKenya in 2008 (Gordon & Barbero, 2008). The species was not sampled during the previous and only known comprehensive inventory of northern Tanzanian dung beetles undertaken by in 1975 (Davis & Dewhurst, 1993).

African dung beetle community dynamics and activity is most likely determined by regional rainfall patterns and fluctuations in temperature with maximum diversity observed after rainfall and decreasing as surface conditions become warmer and drier (Davis, 1996b). This effect of seasonality is widespread across the tropics and in areas that have bimodal distribution in rainfall. Although average annual rainfall distribution in Tanzania is unimodal and is influenced by the Intertropical Convergence Zone, northern Tanzania where this study takes place typically experiences both a dry season, which spans from late June to early October and a wet season, with most of the rainfall occurring during the 'long rains' which fall between Decemeber and May (Borhara et al., 2020). Environmental monitoring is typically a balance between maintinaing adequate sampling effort to detect a statistical signal, while keeping within financial and/or time constraints (Bicknell et al., 2014). While the data presented here is limited to the dry season this research clearly demonstrates the suitability and use of dung beetles as a focal taxonomic group to investigate the effects of disturbance within a restricted timeframe

Implications for Conservation

The results presented here identify which dung beetle species may provide future effective indicators of habitat modification and provide a cost effective and efficient method of ascertaining the direction of ecological

change within African savannah habitats. A study by Engelbrecht (2010) surveyed the value of invertebrate inventories for protected areas in South Africa and found that 97% of park managers and ecologists wished to have a more inventories of invertebrate groups and described the lack of such information as an impediment to effective conservation planning. While only one of the three sites studied here form part of a legally protected area, all of the study sites are located with the Kwakuchinja wildlife corridor; an area under going rapid change with land converted from mixed savannah to agriculture increasing by 35% and woodlands decreasing by 67% in the years 2002 to 2017 (Martin et al., 2019). Our findings suggest that conservation planning for areas undergoing rapid land use change, such as the locations studied here, should concentrate on setting conservation priorities to conserve the functional integrity of taxa such as dung beetles that contribute greatly to ecosystem services provision as well as protecting biodiversity in general.

Data Availability Statement

The data that supports the findings of this study are openly available in the Figshare repository at https://figshare.com/s/0cbea665c53f76a18086

Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

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Supplemental material

Supplemental material for this article is available online.

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