Journal of Insect Conservation (2022) 26:711–720
https://doi.org/10.1007/s10841-022-00410-6

ORIGINAL PAPER

Grass and ground dwelling beetle community responses to holistic and wildlife grazing management using a cross-fence comparison in Western Kalahari rangeland, Namibia

Johanna E. Reinhard[1,2] · **Katja Geissler**[2] · **Niels Blaum**[2]

Received: 29 March 2021 / Accepted: 21 May 2022 / Published online: 7 July 2022
© The Author(s) 2022

Abstract
Savannahs are often branded by livestock grazing with resulting land degradation. Holistic management of livestock was proposed to contribute to biodiversity conservation by simulating native wildlife grazing behaviour. This study attempts the comparison of the impact of a holistic management regime to a wildlife grazing management regime on grass and ground-dwelling beetle species diversity on neighboring farms in Namibian rangeland. Results show that the response of biodiversity in species richness and composition to holistic management of livestock differs substantially from wildlife grazing with a positive impact. From a total of 39 identified species of ground-dwelling beetles (Coleoptera: Tenebrionidae, Carabidae) from 29 genera, eight species were found to be indicators for holistic management of livestock and three were found to be indicators for wildlife grazed rangeland. Observations suggest that holistic management of livestock may contribute to biodiversity conservation, but the differential effect of grazing management on species assemblages suggests that livestock grazing cannot replace native wildlife herbivory.
Implications for insect conservation An adaptive management strategy such as holistic management used in this study shows the potential to support high beetle biodiversity. Holistic management of livestock thus aspects in favour for a sustainable form of grazing management for insect conservation even though it does not functionally replace grazing by native wildlife.

Keywords Beetle conservation · Land use management · Biodiversity · Insect conservation · Wildlife management

Introduction

Savannahs worldwide have been exploited for centuries through livestock grazing. Land degradation due to overgrazing has significantly reduced structural and species diversity (Jeltsch et al. 1997; Blaum et al. 2009), displaced species interactions, triggered cascading effects on trophic groups (Wasiolka and Blaum 2011), prevented gene flow (Blaum and Wichmann 2007) and had negative impact on pastoral land use, causing a significant reduction in economic profitability (Stafford et al. 2017). The negative effects of unsustainable grazing management are expected to be exacerbated by poverty and high human population growth in the future (Eldridge et al. 2011). In Southern Africa, 43% of the land is private because governments commercialized rangeland in order to prevent further degradation (Kgosikoma et al. 2013). To date the most common management practice on commercial farms is a fixed rotational grazing scheme. Rotational management varies in grazing time and stocking rate, but generally, livestock is split into several herds and rangeland is demarcated with inner fences for paddocks. Livestock herds are kept in paddocks and left to graze. Moving to the next, the grazed paddock is left to rest until the next herd reaches the paddock to re-graze. Yet, degradation in the form of bush encroachment continues and intensive grazing management of livestock needs continuous reinvention to sustain rangeland productivity (Eldridge et al. 2011). Recently, a call for an adaptive grazing management strategy has been made in order to completely eliminate or prevent the degrading grazing impact on the ecosystem (Fynn et al. 2016; Jakoby et al. 2015; Wallgren et al. 2009).

✉ Johanna E. Reinhard
jrbiologie@gmail.com

[1] Leibniz-Institut of Freshwater Ecology and Inland Fisheries, Müggelseedamnn 310, 12587 Berlin, Germany

[2] Institut Für Biochemie Und Biologie, Plant Ecology and Nature Conservation, University of Potsdam, am Mühlenberg 3, 14476 Potsdam, Germany

Both, holistic management of livestock and native ungulate grazing in the form of wildlife management pose management options contributing to biodiversity conservation.

Adaptive holistic livestock management was proposed to restore degraded grasslands and improve fodder production for livestock under the hypothesis where densely stocked livestock mimics native ungulate grazing and herding behaviour (Savory and Parson 1980; Savory and Buttefield 1998). Wildlife foraging pattern is characterized by a high spatial and temporal variability in forage quantity and quality. Holistic management endeavours to achieve this by rotational management with short-term intensive grazing followed by very long rests from grazing. Holistic management is recently applied by landowners of savannah rangelands in Southern Africa and in the USA even though its management scheme has received much criticism (e.g. Carter et al. 2014). Details on stocking rates, allowable use of livestock and amount of rested recovery is individually set and permanently reset by the landowner. Its adaptive nature is a reason why the effects on the ecosystem and biodiversity are difficult to evaluate in holistic management (Carter et al. 2014; Farrié et al. 2015; Briske et al. 2014).

While land use pressure in Africa has been increasing due to poverty and population growth, the change in land use type from domestic livestock towards wildlife farming has led to a significant increase in the number of conservancies (Lindsey et al. 2013). Wildlife farming has the potential to contribute to biodiversity conservation (McGranahan 2008; Blaum et al. 2009) and regulate long-term wood and grass demography (Sankaran et al. 2013; Augustine and Mcnaughton 2004). It was identified as being resilient to climate change and better adapted to local environmental conditions; not to mention that native ungulates are considered to be under threat themselves, as the management of livestock is displacing the persistence of native wild ungulates in African savannahs (Veblen and Young 2010; Fynn et al. 2016; Young et al. 2005). Furthermore, for the mix of grazing behaviour by multiple species and their optimal use of vegetation and lower water footprint, it was proposed that native ungulates can be kept at high stocking density (Muir 1989) in a large area with income generated from ecotourism, safari, hunting and meat production (Lindsey et al. 2013). Management of wildlife mainly encompasses accurate estimates of population sizes and the artificial reduction of animal numbers in order to avoid overgrazing and competition for resources. Wildlife management requires comparatively little habitat rearrangement (i.e. building of inner fences and water reservoirs) to management of livestock management (Bothma and du Toit 2010).

Although both, contemporary holistic management of livestock and management of native ungulates are promising management strategies safeguarding arid savannah rangelands, studies explicitly analysing the value for insect biodiversity conservation on savannahs are scarce. The individuality of management regimes employed by private landowners often make it difficult to scientifically evaluate the impact. This is especially true for the impacts of management induced vegetation changes on animal diversity. Invertebrates, in particular, display strong responses to seasonality and environmental conditions, often more than vertebrates including migratory and/or diapause behaviour (Wolda 1988) and are thus promising indicators for assessing the potential of savannah management strategies. Flightless beetles are sensitive to changes in structural diversity and small scale habitat changes, easy to sample and extremely species rich in arid systems (Blaum et al. 2009; Wasiolka and Blaum 2011; Woodcock et al. 2005). Among Coleoptera, darkling beetles (Tenebrionidae) are the fifth largest family of beetles with approximately 19,000 described species worldwide (Aalbu et al. 2002; Scholtz and Holm 1985) dominating arid ecosystem insect faunas. They often are scavengers living on or in sandy soils under leaf litter and play the role of ecosystem engineers (Megías et al. 2011). Ground beetles (Carabidae) were shown to be good ecological indicators for biodiversity in many ecosystems ((Yanahan and Taylor 2014; Rainio and Niemelä 2003; McGeoch et al. 2002).

This is the first study that makes initial observations comparing the impact of holistic management of livestock to native wildlife management on beetle biodiversity of two neighbouring farms with similar edaphic and climatic conditions. If holistic management of livestock effectively mimics ungulate grazing behaviour under wildlife management, the response of biodiversity is expected to be similar between the two management options. This study provides initial insights into using a cross-fence example to assess the impact of holistic livestock and wildlife management on grass and ground-dwelling beetle communities in arid savannah rangeland in Namibia.

Methods

Study sites

Beetle and grass communities were studied in 2015 on wildlife grazed rangeland (Kuzikus: S 0232971; E 7427778) and domestic grazed rangeland with holistic management of livestock (Achab: S 0228022; E 742955) situated at the edge of the Kalahari Desert in Namibia.

The total abundance on wildlife reserve Kuzikus is estimated to 4500 animals including 14 species of native ungulates: *Antidorcas marsupialis* (Springbok), *Oryx gazella* (Gemsbok), *Damascus phillipsi* (Blessbok), *Alcelaphus buselaphus* (Hartebeest), *Equus zebra* (Zebra), *Connochaetes taurinus (*blue Wildebeest), *Connochaetes gnou* (black Wildebeest), *Aepyceros melampus* (Impala), *Taurotragus oryx* (Eland), *Giraffa camelopardilis* (Giraffe), *Strepsiceros cottoni*

(greater Kudu), *Sylvicarpa grimmia* (Duiker). *Raphicerus campestris* (Steenbok) and *Diceros bicornis* (black Rhino). Considering the average weights of animal species, excluding black rhino, across the year, the stocking rate on Kuzikus was equal to 51.46 kg/ha (wet animal weight per hectare); a comparable measure to the production of livestock on the neighbouring holistically managed farm. Animals freely roam the area of 10,500 hectares which is fenced. Wildlife investigated plots were considered to have continuous grazing pressure by wild ungulates during February (summer, growing season), May (winter) and August (dry season).

Across the fence, Achab/Springbokvlei manages domestic livestock (4741 animals) in fenced grazing areas (camps) of 155 ha in a rotational manner on a total area of 9000 ha producing 41.18 kg/ha in total. Following a holistic management approach, livestock is herded and kept in camps for 14 days for short term intensive grazing with a grazing pressure of 1122 kg/ha of sheep weight in February (summer, growing season) and 777 kg/ha of cattle weight in August (dry season). Camps rested for 6 months from grazing with no grazing in May (winter).

Beetle and vegetation surveys

Data were collected for three seasons separately within a period of three to four weeks in February 2015 (summer, growing season), May 2015 (beginning of winter) and August 2015 (dry season) on both management types. Twelve 5 × 5 m plots were surveyed per study site and season. Beetles were collected in pitfall traps placed in the middle of a 5 × 5 m plot and vegetation was sampled within each 5 × 5 m plot around the pitfall trap. A pitfall trap was a bucket with 33 cm radius and 40 cm depth, dug deep into sand without rims, so insects could fall in easily. Rarefaction of the beetle data showed that a period of 4 days was sufficient to adequately depict the Coleopteran community. Traps were emptied after four days and all Tenebrionidae and Carabidae were counted and identified to species. Vegetation was surveyed at the time of pitfall collection and comprised the estimation of percentage cover of bare ground, total vegetation and litter, as well as the number of grass species and percentage cover for each species.

Statistical analysis

A linear model (ANOVA) was used for comparing species numbers of grasses and beetles between seasons and management types. Significant terms were detected using stepwise backward elimination. To compare composition of species assemblages, *k-means* clustering and non-metric multidimensional scaling (NMDS) using Bray–Curtis dissimilarity matrix (Bray and Curtis 1957). Analysis of Similarity (ANOSIM) (Chapman and Underwood 1999) and PERMANOVA were used to test for significant differences in assemblage composition between management types. PERMANOVA ist more robust than ANOSIM und useful because it is largely unaffected by heterogeneity in distances. Indicator species analysis (function IndVal) was used on beetle samples pooled across the year, to eliminate seasonal abundance differences and activity patterns. IndVal measures the degree of specificity (relationship of a species with a specific variable) and the degree of species fidelity (every time that some condition was met, the species was present) in relation to management type. All statistics were performed using R 3.2.5 (R Core Team. 2014).

Results

Species accumulation curves show the differences in species numbers for grasses and beetles per management type between seasons (Fig. 1).

A total of 16 grass species were identified, of which all were found on holistic management sites. Six species were found on wildlife grazed rangeland (Table 1).

A total of 563 Coleoptera specimens belonging to 39 species from 29 genera were collected and identified, out of which 28 belong to the family Tenebrionidae and 11 to the family Carabidae (Table 2). In total, 20 species were found on wildlife grazed rangeland of which six species were unique to the treatment. 33 species were found in holistic management rangeland with 18 unique species (Table 2).

The grass and beetle communities differed in both, species number (Fig. 2) and composition (Fig. 3) between holistic and wildlife management throughout the year. Wildlife managed sites were lower in grass species richness than holistically managed sites with a significant interaction between season and management type (ANOVA, $F = 22.5$, $p < 0.001$, $df = 2$, Fig. 2).

Beetle species richness differed significantly between management types (ANOVA, $F = 14.81$, $p < 0001$, $df = 2$, Fig. 2). Under holistic management, beetles species richness peaked slightly in May and on wildlife managed rangeland, the number of grass species was greatest in February (Fig. 2). In wildlife managed sites, beetle species were most numerous in August (Fig. 2). Management has a significant influence species composition of both grasses (PERMANOVA, $F = 9.96$, $p < 0.001$, $df = 5$) as well as of beetles (PERMANOVA, $F = 6.09$, $p < 0001$, $df = 5$), where clear clusters of species assemblages can be visualised between management types in all seasons (Fig. 3).

Three beetle indicator species characteristic for wildlife grazed rangelands were identified with IndVal (all belong to the genus *Zophosis*, Table 2). In total, eight beetle species were identified as indicators for holistic management of livestock, of which five belong to the tribe Eurychoriini with described

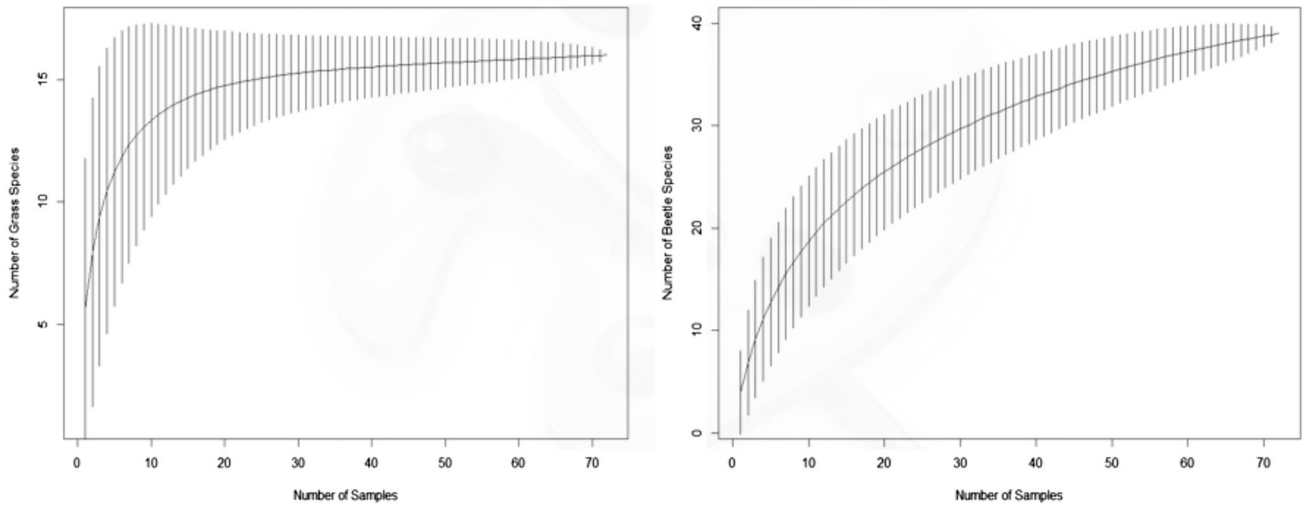

Fig. 1 Species accumulation curves of the total nummer of beetle and grass species captured indicating the adequacy of the fauna and flora survey in the study sites

Table 1 Grass species list and their mean percentage cover per plot (Mean ± Standard Error (SE), n = 36) from each management type (Holistic versus Wildlife) across the year, sorted by the most abundant species from holistic management sites

Species	Holistic (Mean ± SE)	Wildlife (Mean ± SE)	Palatability. nutritional value. successional status[a]
Stipagrostis uniplumis	24.56 ± 2.89	0.56 ± 0.42	Palatable. good. sub-climax
Aristida stipitata	14.14 ± 1.78	15.61 ± 3.42	Unpalatable. low. pioneer or sub-climax
Aristida congesta	5.86 ± 1.07	3.17 ± 0.52	Intermediate. poor in dry season. Pioneer
Pogonothria fleckii	2.86 ± 1.71	0.47 ± 0.12	Very low. very poor. Pioneer
Schmidtia kalahariensis	1.75 ± 0.20	2.08 ± 0.31	Unpalatable. high. Pioneer
Eragrostis lehmanniana	1.03 ± 0.42	–	–
Eragrostis cylindriflora	1.03 ± 0.18	0.94 ± 0.39	Palatable. good. sub-climax
Aristida meridionalis	0.67 ± 0.08	–	Palatable when young. low. Climax
Stipagrostis ciliata	0.61 ± 0.11	–	Very palatable. high. sub-climax
Eragrostis triphora	0.50 ± 0.10	–	Very palatable. very high. Climax
Digitaria vulgaris	0.47 ± 0.12	–	–
Eragrostis annulata	0.28 ± 0.11	–	Low palatability. low. Pioneer
Eragrostis biflora	0.25 ± 0.11	–	–
Eragrostis rotifer	0.22 ± 0.12	–	Intermediate. intermediate. sub-climax
Eragrostis porosa	0.19 ± 0.07	–	Intermediate. intermediate. sub-climax
Cenchrus ciliaris	0.08 ± 0.08	–	Palatable. high. Climax

[a]Roodt (2015)

Stips dohrni, *Renatiella scrobipennis*, *Eurychora nitida*, *Gonopus deplanatus* and three Carabidae, including described *Cypholoba gracilis* and *Attractonotus mulsanti* (Table 2).

Discussion

The current study is the first attempt to assess the potential of holistic livestock management for biodiversity conservation in arid savannah rangelands in comparison to cross-fence wildlife grazing. The concept of mimicking grazing behaviour of native wildlife in the holistic management approach is clearly rejected by this study: grass and ground-dwelling beetle species and assemblages differed significantly between holistic livestock and wildlife management.

Morris (2000) highlighted the complexity of the interactions of arthropods with different types of grazing management. He showed that there is a requirement to determine the effects on arthropods of different grazing types, but broken

Table 2 Ground dwelling beetle species with number of captures per management type (holistic vs wildlife) in subtotals, mean abundances per trap (Mean SE) across one year including indicator species results

Family	Tribe	Species	Holistic			Wildlife						
			Mean	SE	Subtotal	MEAN	SE	Subtotal	IndVal	*p*	*sig*	Total
Carabidae												
1	Anthiini	*Anthia cinctipennis* (Lequien, 1832)	0.08	0.06	3	–	–	0	0.194	0.804		3
2	Anthiini	*Attractonotus mulsant* (Perroud, 1846)	0.17	0.10	6	–	–	0	0.238	0.569		6
3	Anthiini	*Cypholoba fritschi (Chaudoir, 1883)*	0.03	0.03	1	–	–	0	0.137	1.000		1
4	Anthiini	*Cypholoba gracilis* (Dejean, 1831)	0.53	0.20	19	–	–	0	0.412	0.116		19
5	Anthiini	*Thermophilium aemiliana* (Dohrn, 1821)	0.08	0.06	3	–	–	0	0.194	0.813		3
6	Anthiini	*Triaenogenius corpulentus* (Chaudoir, 1877)	0.03	0.03	1	–	–	0	0.137	1.000		1
7	Helluonini	*Gonogenia immitera kalaharica* (Basilewsky, 1980)	–	–	0	0.03	0.03	1	0.229	0.280		1
8	Manticorini	*Manticora* (Fabricius,1781)	0.06	0.04	2			0	0.194	1.000		2
9	Scaritini	*Passalidius fortipes* (Boheman, 1860)	–	–	0	0.06	0.04	2	0.194	1.000		2
10		CA011	–	–	0	0.03	0.03	1	0.229	0.260		1
11		CA054	0.31	0.12	11	–	–	0	0.363	0.178		11
Tenebrionidae			–	–								
12	Adesmiini	*Renatiella scrobipennis (Haag-Rutenberg, 1875)*	0.33	0.09	12	0.08	0.05	3	0.514	0.030	*	15
13	Cryptochilini	*Pachynotelus (Solier.1840)*	0.11	0.05	4	–	–	0	–	–		4
14	Eurychorini	*Eurychora nitida (Haag-Rutenberg.1875)*	0.39	0.21	14	0.06	0.04	2	0.334	0.434		16
15	Eurychorini	*Geophanus sp.22 (Haag-Rutenberg.1875)*	0.03	0.03	1	0.00	0.00	0	–	–		1
16	Eurychorini	*Stips dohrni (Haag-Rutenberg)*	0.75	0.22	27	0.14	0.07	5	0.535	0.067		32
17	Molurini	*Decoriplus hieroglyphicus (Haag-Rutenberg.1875)*	0.11	0.05	4	0.11	0.07	4	–	–		8
18	Platynotini	*Gonopus agrestis*	0.08	0.05	16	–	–	0	–	–		16
19	Platynotini	*Gonopus tibialis (Fabricius.1798)*	0.44	0.11	3	–	–	0	–	–		3
20	Scaurini	*Herpiscius sp.38*	0.06	0.04	2	–	–	0	0.194	1000		2
21	Sepidiini	*Pasmmodes sp.25 (Kirby.1819)*	0.06	0.04	2	–	–	0	0.194	1000		2
22	Sepidiini	*Psammodes sp.26 (Kirby.1819)*	0.03	0.03	1	–	–	0	0.137	1.000		1
23	Sepidiini	*Psammodes vialis (Burchell.1822)*	0.08	0.06	3	–	–	0	0.194	0.796		3
24	Sepidiini	*Somaticus aenus* (Solier.1843)	–	–	0	0.06	0.04	2	0.194	1.000		2
25	Zophosini	*Zophosis (Halogenosis) burkei burkei (deyrole.1867)*	0.14	0.07	24	0.81	0.21	161	0.930	0.001	***	185
26	Zophosini	*Zophosis (Halogenosis) burkei rufipennis (Deyrolli.1867)*	–	–	0	0.42	0.14	15	0.538	0.003	**	15
27	Zophosini	*Zophosis amita (Penrith.1977)*	0.14	0.11	5	0.06	0.04	2	0.275	0.464		7
28	Zophosini	*Zophosis deyrolli (Lucas.1867)*	0.67	0.22	8	4.47	0.51	21	0.657	0.002	**	29
29	Zophosini	*Zophosis jakoti (Penrith.1981)*	0.86	0.18	5	1.56	0.54	29	0.573	0.014	*	34
30	Zophosini	*Zophosis kochi (Penrith.1977)*	0.22	0.07	31	0.58	0.15	56	–	–		87
31	Zophosini	*Zophosis sp.6*	0.03	0.03	1	0.03	0.03	1	0.194	1.000		2
32		TE021	0.25	0.09	9	0.11	0.05	4	0.391	0.257		13
33		TE064	0.06	0.04	2	–	–	0	0.194	1000		2

Table 2 (continued)

Family	Tribe	Species	Holistic			Wildlife			IndVal	*p*	*sig*	Total
			Mean	SE	Subtotal	MEAN	SE	Subtotal				
34		TE065	0.14	0.09	5	0.14	0.07	5	0.137	1.000		10
35		TE066	0.11	0.07	4	0.22	0.10	8	–	–		12
36		TE067	0.22	0.08	8	0.03	0.03	1	–	–		9
37		TE068	0.03	0.03	1	–	–	0	0.137	1.000		1
38		TE072	0.03	0.03	1	–	–	0	0.137	1.000		1
39		TE075			0	0.03	0.03	1	0.137	1.000		1
	Total count				*239*			*324*				*563*

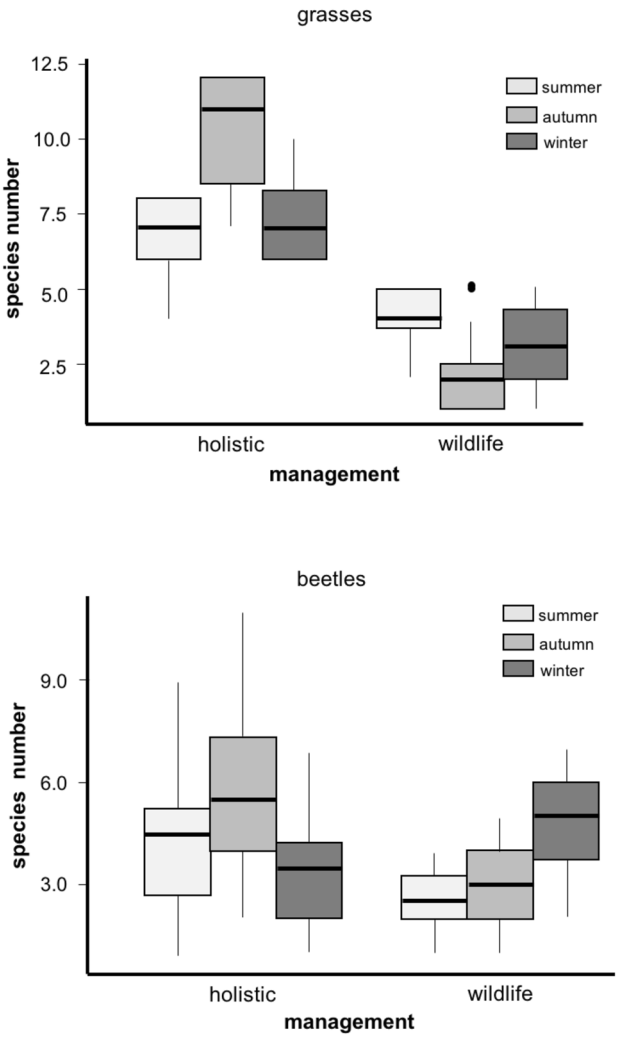

Fig. 2 Box plot of the impact of management type and season on species richness of **1**) grasses and **2**) beetles on holistic livestock and wildlife management. Mean count values of species number ± standard deviation are shown in February (light grey), May (grey) and August (dark grey)

down into basic components of grazing species, grazing intensities, and the temporal aspects of grazing. Consequent research showed that management regimes do not directly affect arthropod abundance and richness but that grazing induced plant diversity influences arthropod communities (Woodcock et al. 2005). In this study, the higher species richness and abundance of beetles found under holistic management is likely to be the result of increased species richness of grazing induced vegetation. Altered grass tuft sizes, root biomass, soil quality and seed availability are all resources that are likely to provide shelter, hide and food to ground dwelling beetles and cause cascading changes in beetle fauna. Vegetation structure induced by grazing management can thus explain the coleopteran community richness,

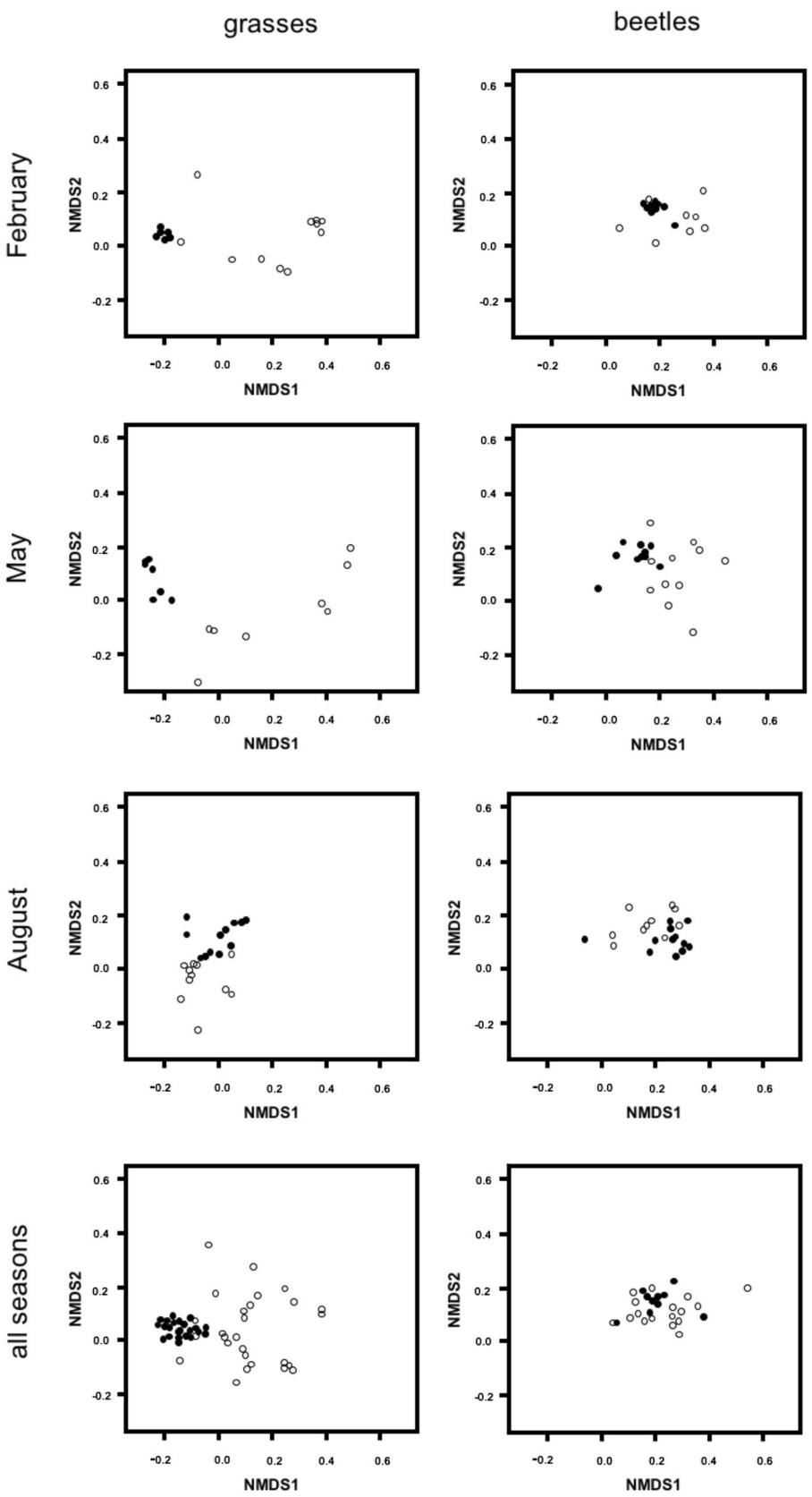

Fig. 3 Seasonal changes in species composition of grasses and beetles for two management types. Non-metric multidimensional scaling (NMDS) showing species compositional clusters in seasons of **1**) grasses and **2**) beetles collected from **a**) February, **b**) May and **c**) August and **d**) across all seasons in holistic (open circles) and wildlife (closed circles) management

under the aspect that greater resources are available for the coexistence of more species (Hart and Horwitz 1991).

Stocking rate plays an important role in the formation of vegetation structure and its associated cascading effects on fauna (McGranahan and Kirkman 2013). In this study, however, cascading effects on composition and species richness were visible despite similar stocking rates of wildlife and livestock. This can be attributed to differences in herbivore grazing behaviour between sheep, cattle and wildlife. Here, single species grazing under holistic management of livestock had a positive impact on grass richness and promoted palatable and nutritious grassland (i.e. *Stipagrostis uniplumis*) compared to wildlife grazing, which stands in contrast to a positive influence on ecosystem functioning by herbivory consisting of native wild ungulates (Prins and Fritz 2008). It is well recognised, that mono-specific herbivory, such as grazing by cattle or sheep, having replaced former wildlife communities, has led to an imbalance of grass/tree vegetation through large-scale overgrazing and therefore bush encroachment (van Langevelde et al. 2003; Ritchie and Olff 1999). Seasonal adaptation of management to livestock herbivore behaviour in the holistic management scheme, as practiced in this study, however, benefits biodiversity. It implements intensive sheep grazing (2 weeks) during growing season in the summer (February), includes a long rest from grazing (6 months) and continues with intensive cattle grazing (2 weeks) in winter (August). Small-bodied and narrow-mouthed herbivores constrain forage to selection for rarer high-quality grasses as they are better able to select higher quality green leaves and avoid low quality stems and dead leaves on taller grasses. They (i.e. goats, sheep, impala, springbok) have low absolute food requirements and a preference for short grasslands (Vallentine 2000). After intense grazing in the growing season, saplings had time to re-sprout for six months due to grazing rest. Grazing rest also raised the opportunity for grass species that are highly palatable and nutritious for livestock to recover and grow evenly. It was shown previously that long term rest from livestock grazing can lead to overall grass biodiversity increase (Carter et al. 2014 and references therein). A resulting species-rich and tall grassland was surveyed at the end of the growing season (May) at holistic managed sites. Cattle were left to graze after recovery when grassland was tall. Cattle have relatively wide mouths, but their large body size and the use of their tongue sweep strategy to increase bite size constrain them to optimal foraging in intermediate to tall grasslands (Fynn et al. 2016). In comparison, native ungulate guilds under wildlife management consisted of a variety of small-bodied and narrow-mouthed selective grazers like springbok, blessbok, hartebeest and gemsbok with a preference for short grass and broad mouthed herbivores, like zebra and wildebeest which are more efficient at foraging on short, dense swards and have a preference for intermediate grasslands. Wildlife forages all year round and seasonal grazing was shown to have a considerable impact on Carabid beetles (Reinhard et al. 2018). Contrary to holistic management of livestock, continuous grazing of native ungulates resulted in only a few grass species (i.e. *Aristida stipitata*) that are resistant to grazing but unpalatable and of low nutritious value to livestock (refer to Table 1). However, wildlife is able to persist on this low nutritious grassland, owing to their respective mouth anatomy and body size. Most native ungulates are able to maximise their energy intake on grass swards of less than 100 gm^{-2} (Fynn 2012). Previously it was shown that under livestock management, rotational grazing schemes and intense management neither increased animal production nor protected rangeland from degradation any more than continuous grazing without rotation (Kgosikoma et al. 2013). Upon this, even though domestic and wild herbivores compete for the same resources (Prins 2000), their different feeding strategy and mouth anatomy influence the response in biodiversity.

A closer look at indicator species shows that under wildlife grazing, endemic *Zophosini* predominate and are highly specific to the habitat. It was shown previously that Zophosini prefer low shrub cover (Hering et al. 2019) and are highly sensitive to grazing, fire and their interaction (Reinhard et al. 2018). All *Zophosini* are morphological extremely similar to each other; their ecology in arid environments is hardly described, but their small size and fast-moving behaviour implies their adaptation to heat and poor vegetation with little cover characteristic for continuously wildlife grazed sites. Furthermore, a thorough hebacous layer may provide a nutritional and diverse litter layer, that a diversity of Tenebrionidae decompose in dry season (Hering et al. 2019). For example, *Zophosis (Halogenosis) burkei rufipennis* is a species absent in holistic management sites, reddish in colour and hardly visible on bare ground; it is diurnal and fast-moving (Reinhard *pers. Obs.*) and closely related to *Zophosis (Halogenosis) burkei burkei.* Both species were found to be indicators for wildlife management in this study. *Zophosis (Halogenosis) burkei burkei* (TE003 in Hering et al. 2019) was described to be a niche specialist for high shrub cover on conventional cattle managed farm, where areas in high shrub cover are usually low in grass cover and food shortage (Hering et al. 2019). *Zophosis (Hologenosis) burkei* subspecies have increased body weights in grazed conditions after fire, which refelcts their preference for simple niches (Reinhard et al. 2018), supporting the idea of being indicators for conitnous wildlife grazed rangeland. *Eurychora nitida* and *Stips dohrni*, indicators for holistic management, have a flattened body shape and are slow-moving. They belong to the Old World tribe *Eurychorini* which is also described, together with *Zophosini* and *Adesmiini*, as adapted to extreme conditions to the sandy areas (Penrith 1984). *Eurychora* and *Stips* are genera widely distributed in Southern Africa

(Louw 1979). Species specific information is scarce, however, a study by Louw (1979) compared species composition between the Namib and Kalahari Desert and described ecological equivalents in the ground-living Tenebrionidae between the deserts, demonstrating adaptational differences to habitats even within tribes. *Renatiella scrobipennis*, endemic to the Kalahari Desert, is active during winter and diurnal with a preference for vegetated, rhigozum plains (Louw 1979, 1983). Caraboid species found in this study live under decaying plant material such as logs or leaf litter, and some prefer open sandy patches among tufts of grasses (Reinhard *pers. obs.*). Nearly all species of Carabidae are predators. *Cypholoba gracilis* and *Attractonotus mulsanti*, indicators found for holistic management, belong to the tribe *Anthiini*, which are especially numerous in the Karoo and Kalahari (Mawdsley et al. 2012). The potential of *Anthiini* to be incorporated into environmental monitoring programs has been recognised previously due to their close association with vegetation communities and their activity patterns being closely linked to temperature, season and rainfall (Schmidt 2001). In a previous study, we have identified the detrimental effect grazing can have on Carabidae in dry season (Reinhard et al. 2018). However, information on the biology of single species is scarce and warrants greater attention.

In conclusion, this study exemplified that holistic management of livestock exerts a considerable different effect on species richness and composition of plant and cascading beetle communities compared to wildlife grazing in arid savannah. Beetles were shown to be promising bio indicators for rangeland management, as the assemblages of beetle indicator species clearly showed that neither holistic management of livestock nor management of wildlife is functionally replaceable or comparable in an arid savannah ecosystem. Food requirements, feeding strategy and mouth anatomy of ungulate grazers might influence the grazing impact on biodiversity. Adapted accordingly (i.e. to seasons), holistic management of livestock, with a reference to the management applied in this particular study, has the potential to support a high biodiversity. Holistic management of livestock thus aspects in favour for a sustainable form of grazing management though not functionally replacing grazing by native wildlife.

Acknowledgements We acknowledge Dawid Sczymroszyck for his help on Tenebrionidae and Carabidae species identification, landowners Berend Reinhard and Judith Isele for their support and access to study sites and the Ministry of Environment and Tourisms Namibia for research permission in the study areas (1738/2012).

Funding Open Access funding enabled and organized by Projekt DEAL. This study was funded by the DAAD (91541055) and by the German Federal Ministry of Education and Research (BMBF) in the framework of the SPACES project OPTIMASS (FKZ 01LL1302A).

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

Aalbu RL, Triplehorn CA, Campbell JM, Brown KW, Somerby RE, Thomas DB (2002) Tenebrionidae. In: Arnett RH, Thomas MC, Skelley PE, Frank JH (eds) American Beetles. Vol. 2. Polyphaga: Scarabaeoidea through Curculionoidea. CRC Press, Boca Raton, pp 463–500

Augustine DJ, Mcnaughton SJ (2004) Regulation of shrub dynamics by native browsing ungulates on East African rangeland. J Appl Ecol 41(1):45–58

Blaum N, Wichmann MC (2007) Short-term transformation of matrix into hospitable habitat facilitates gene flow and mitigates fragmentation. J Anim Ecol 76(6):1116–1127

Blaum N, Seymour C, Rossmanith E, Schwager M, Jeltsch F (2009) Changes in arthropod diversity along a land use driven gradient of shrub cover in savanna rangelands: identification of suitable indicators. Biodivers Conserv 18(5):1187–1199

Bothma JP, du Toit JG (2010) Game Ranch management. Van Shaik Publishers, Pretoria

Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. Ecol Monogr 27(4):325–349

Briske DD, Ash AJ, Derner JD, Huntsinger L (2014) Commentary: a critical assessment of the policy endorsement for holistic management. Agric Syst 125:50–53

Carter J, Jones A, O'Brien M, Ratner J, Wuerthner G (2014) Holistic management: misinformation on the science of grazed ecosystems. Int J Biodivers 2014:1–10

Chapman MG, Underwood AJ (1999) Ecological patterns in multivariate assamblages: information and interpretation of negatiove values in ANOSIM tests. Mar Ecol Prog Ser 180:257–265

Eldridge DJ, Bowker MA, Maestre FT, Roger E, Reynolds JF, Whitford WG (2011) Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. Ecol Lett 14(7):709–722

Farrié B, Jouven ML, Moreau J-C, Moulin C-H, Piquet M, Taverne M, Tchakérian E, Thénard V, Martin G (2015) Rangeland Rummy—a board game to support adaptive management of rangeland-based livestock systems. J Environ Manage 147:236–245

Fynn RWS (2012) Functional resource heterogeneity increases livestock and rangeland productivity. Rangeland Ecol Manage 65:319–329

Fynn RWS, Augustine AJ, Peel MJS, de Garine-Wichatitsky M (2016) Strategic management of livestock to improve biodiversity

conservation in African savannas: a conceptual basis for wildlife-livestock coexistence. J Appl Ecol 53:388–397
Hart DD, Horwitz RJ (1991) Habitat diversity and the species—area relationship: alternative models and tests. In: Bell SS, McCoy ED (eds) Habitat structure. Springer, Netherlands, pp 47–68
Hering R, Hauptfleisch M, Geißler K, Marquart A, Schoenen M, Blaum N (2019) Shrub encroachment is not always land degradation: insights from ground-dwelling beetle species niches along a shrub cover gradient in semi-arid Namibian savanna. Land Degrad Dev 30:14–24
Jakoby O, Quaas MF, Baumgärtner S, Frank K (2015) Adapting livestock management to spatio-temporal heterogeneity in semi-arid rangelands. J Environ Manage 162:179–189
Jeltsch F, Milton S, Dean W, Van Rooyen N (1997) Analysing shrub encroachment in the Southern Kalahari: a grid-based modelling approach. J Appl Ecol 34(6):1497–1508. https://doi.org/10.2307/2405265
Kgosikoma OE, Mojeremane W, Harvie BA (2013) Grazing management systems and their effects on savanna ecosystem dynamics: a review. J Ecol Nat Environ 5(6):88–94
Lindsey PA, Balme G, Becker M, Begg C, Bento C, Bocchino C et al (2013) The bushmeat trade in African savannas: impacts, drivers, and possible solutions. Biol Conserv 160:80–96
Louw S (1979) MSc-Thesis. Ecological equivalence and phylogeny of Tenebrionidae (Coleoptera) as indicators of the connection between Namib and Kalahari dunes. Navorsinge van die Nasionale Museum, Bloemfontein 5:12
Louw S (1983) The diversity and day and seasonal activity of ground-living Tenebrionidae (Coleoptera) in the southern Namib and Kalahari ecosystems. Cimbebasia (a) 7:36–56
Mawdsley JR, Erwin TL, Sithole H, Mawdsley AS (2012) A synopsis of the genus Cypholoba Chadoir (Coleoptera, Carabidae, Anthiini) know to occur in the Republic of South Africa. Zookeys 181:23–43
McGeoch MA, van Rensburg BJ, Botes A (2002) The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem. J Appl Ecol 39:661–672
McGranahan DA (2008) Managing private, commercial rangelands for agricultural production and wildlife diversity in Namibia and Zambia. Biodivers Conserv 17(8):1965–1977
McGranahan DA, Kirkman KP (2013) Multifunctional Rangeland in Southern Africa: managing for production, conservation, and resilience with fire and grazing. Land 2:176–193
Megías AG, Sánchez-Piñero F, Hódar JA (2011) Trophic interactions in an arid ecosystem: from decomposers to top-predators. J Arid Environ 75(12):1333–1341
Morris MG (2000) The effects of structure and its dynamics on the ecology and conservation of arthropods in British grasslands. Biol Conserv 95(2):129–142
Muir K (1989) The potential role of indigenous resources in the economic development of arid environments in sub-saharan Africa: the case of wildlife utilization in Zimbabwe. Soc Nat Resour 2(1):307–318
Penrith ML (1984) Origin of sand-adapted tenebrionid beetles of the Kalahari. Koedoe 27:153–165
Prins HH (2000) Competition between wildlife and livestock in Africa. In: Prins HHT, Dolan TT (eds) Wildlife conservation by sustainable use. Springer, Dordrecht, pp 51–80
Prins HH, Fritz H (2008) Species diversity of browsing and grazing ungulates: consequences for the structure and abundance of secondary production. The ecology of browsing and grazing. Springer, Berlin, pp 179–200
R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
Rainio J, Niemelä J (2003) Ground beetles (Coleoptera: Carabidae) as bioindicators. Biodivers Conserv 12(3):487–506
Reinhard JE, Geissler K, Blaum N (2018) Short-term responses of darkling beetles (Coleoptera: Tenebrionidae) to the effects of fire and grazing in savannah rangeland. Insect Conserv Divers 12:39–48. https://doi.org/10.1111/icad.12324
Ritchie ME, Olff H (1999) Spatial scaling laws yield a synthetic theory of biodiversity. Nature 400(6744):557–560
Roodt V (2015) Grasses and grazers of Botswana and the surrounding savanna. Penguin, Cape Town
Sankaran M, Augustine DJ, Ratnam J (2013) Native ungulates of diverse body sizes collectively regulate long-term woody plant demography and structure of a semi-arid savanna. J Ecol 101:1389–1399
Savory A, Parson SD (1980) The Savory grazing method. Rangelands 2:234–237
Savory A, Butterfield J (1998) Holistic management: a new framework for decision making. Island Press, Washington, DC
Schmidt AD (2001) Experimentelle und freilandökologische Untersuchungen zu Aktivitätrhythmik und mikroklimatischem Präferenzverhalten ausgewählter afrikanischer Laufkäferarten der Gattung Anthia und Thermophilum. Mitt Int Entomol Ver Frankf 26(1/2):53–84
Scholtz CH, Holm E (1985) Insects of Southern Africa. Butterworth Publishers Ltd, Durban
Stafford W, Birch C, Etter H, Blanchard R, Mudavanhu S, Angelstam P et al (2017) The economics of landscape restoration: benefits of controlling bush encroachment and invasive plant species in South Africa and Namibia. Ecosyst Serv 27:193
Vallentine JF (2000) Grazing management. Elsevier, Amsterdam
Van Langevelde F, Claudius ADM, van de Vijver KL, Van de Koppel J, De Ridder N, Van Andel J et al (2003) Effects of fire and herbivory on the stability of Savanna ecosystems. Ecology 84(2):337–350
Veblen KE, Young TP (2010) Contrasting effects of cattle and wildlife on the vegetation development of savannah landscape mosaic. J Ecol 98:993–1001
Wallgren M, Skarpe C, Bergstrom R, Danell K, Bergstrom A, Jakobsson T, Karlsson K, Strand T (2009) Influence of land use on the abundance of wildlife and livestock in the Kalahari, Botswana. J Arid Environ 73:314–321
Wasiolka B, Blaum N (2011) Comparing biodiversity between protected savanna and adjacent non-protected farmland in the southern Kalahari. J Arid Environ 75(9):836–841
Wolda H (1988) Insect seasonality: why? Annu Rev Ecol Syst 19(1):1–18
Woodcock BA, Pywell RF, Roy DB, Rose RJ, Bell D (2005) Grazing management of calcareous grasslands and its implications for the conservation of beetle communities. Biol Conserv 125(2):193–202
Yanahan DA, Taylor SJ (2014) Vegetative communities as indicators of ground beetle (Coleoptera:Carabidae) diversity. Biodivers Conserv 23:1591–1609
Young TP, Palmer TM, Gadd ME (2005) Competition and compensation among cattle, zebras, and elephants in a semi-arid savanna in Laikipia, Kenya. Biol Conserv 122:351–359

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.