

Article

Landscape Transformation Influences Responses of Terrestrial Small Mammals to Land Use Intensity in North-Central Namibia

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Abstract: In this study, we investigate and compare the response patterns of small mammal communities to increasing land use intensity in two study areas: private farmland at the southern boundary of Etosha National Park and smallholder farmland in Tsumeb agricultural area. Species richness, community composition and a standardized capture index (RCI) are compared between sites of (a) increasing grazing pressure of ungulates (Etosha) and (b) increasing conversion of bushland to arable land (Tsumeb). Within each study area, we found clear response patterns towards increasing land use intensity. However, patterns differ significantly between the two areas. Within the less-transformed area (Etosha), high land use intensity results in a decrease in the RCI but not species richness. Small mammal communities remain relatively stable, but ecosystem functions (e.g., bioturbation, seed dispersal) are weakened. Within the more-transformed area (Tsumeb), high land use intensity leads to a decrease in species richness and increasing RCIs of two common pest species. The disappearance of a balanced community and the dramatic increase in a few pest species has the potential to threaten human livelihoods (e.g., crop damage, disease vectors). Our comparative approach clearly indicates that *Gerbilliscus leucogaster* is a possible candidate for an ecological indicator of ecosystem integrity. *Mastomys natalensis* has the potential to become an important pest species when bushland is transformed into irrigated arable land. Our results support the importance of area-specific conservation and management measures in savanna ecosystems.

Keywords: land use; livestock grazing; irrigation-based cropping; lucerne; ecological indicator; *Gerbilliscus leucogaster*; Etosha; rodent pest; Southern Africa

1. Introduction

African savannas are of high ecological relevance, but are also vulnerable to human-induced disturbances [1,2]. Owing to the agricultural potential of grassland systems and a growing human population, there is an increasing trend in the conversion of savanna ecosystems into profitable production systems for livestock or crop farming [3]. This can cause a dilemma between nature conservation and land use [4]. In Namibia, there is a trend to move towards a high performing economy and achieve food security by agricultural intensification [5]. For example, many efforts are being made to significantly expand irrigation-based agronomic production in particular areas of the country. This is the case of the so-called “Maize Triangle”, an area with relatively high precipitation, underground water for irrigation and fertile soils that is demarcated by the towns of Grootfontein, Tsumeb, and Otavi

in north-central Namibia [6]. The expansion of irrigation-based agronomic production is also planned for particular areas in north-central and north-eastern regions of the country by utilizing the Kunene, Kavango, and Zambezi rivers [6]. This proposed agricultural intensification and enlargement of fodder production areas at the expenses of relatively natural savanna ecosystems would have negative consequences for Namibia's grassland habitats that have already been intensified in the past and are influenced by grazing pressure and bush encroachment [7,8]. Cultivating crops for commercial purposes in these areas in the future would make it necessary to "prepare" the land, e.g., by shrubland clearing in order to create the necessary irrigation schemes [9]. However, the ecological consequences of such land conversion remain unclear. Considering the challenges to biodiversity and human well-being, the development of conceptual frameworks for a sustainable rangeland development in north-central Namibia is of great importance [10–12].

While the ecological consequences of a conversion of African savannas into arable land are still poorly understood (see above), the consequences of an increasing grazing pressure, especially in association with livestock farming, have been studied on several occasions. Many authors emphasized that livestock farming strongly influences vegetation and leads to severe anthropogenic-induced degradation of rangeland ecosystems [13,14]. Thus, changes in rangeland conditions are most likely reflected by changes in the vegetation, such as a large-scale conversion of grasslands into shrublands [7,15], which has been observed in many African savanna regions over previous years [2,16]. Vegetation parameters are often used to illustrate land use changes. In addition to vegetation-related changes, it is important to look at less visible parameters driving ecosystem alterations [10]. Therefore, the relations between land use and biodiversity have been studied using different animal taxa [10,17–19]. Large mammals are important regulators of processes within savanna ecosystems [20–23] and have been investigated in terms of their responses to land use-induced disturbances [24]. However, terrestrial small mammals, such as rodents, can have equally important key functions as primary consumers of plant biomass, distributors of seeds, prey animals for other species and indicators for changing abiotic factors through burrowing and impact on nutrient recycling [25]. Environmental changes alter small mammal habitat conditions and quickly affect their abundance, survival and reproductive success [26]. Thus, small mammals can be used as indicators for environmental conditions, providing a valuable context to evaluate land use induced faunal changes [27–29]. Moreover, due to this important ecological function in savanna ecosystems, particular small mammal species could become useful to monitor and indicate ecosystem changes following agricultural intensification. However, several studies suggest that population responses seem not consistent among species and geographical locations. Moreover, the impact of land use changes may not only be a result of the conversion of savannas into arable land, but also the result of the introduction of foreign crop species [30]. While improving the yield and nutritional quality of forage crops through the introduction of allochthonous crop species or varieties from other countries, it is likely that some rodent species might develop their full potential as harmful pest species [31,32], finally affecting overall small mammal species composition and community structure. Rodent-related damage to cereal crops remains a chronic problem for many small-scale farmers in Africa [33] and it is problematic from both an economical and a public health perspective [34,35].

Against this background, the overall objective of our study was to investigate and compare the response patterns of small mammal communities to increasing land use intensity within two different areas in northern Namibia: farmland at the southern boundary of Etosha National Park vs. farmland in Tsumeb agricultural area. Each area represents a different degree of landscape transformation and a different nature of increasing land use intensity (grazing pressure vs. conversion into arable land). We applied this comparative approach to investigate, whether the respective small mammal communities show similar or case-specific response patterns towards increasing land use intensity. The degree of similarity or case-specificity of response patterns towards land use intensity has far-reaching implications for the development of management measures concerning savanna ecosystems. Moreover, the comparative approach might help to identify particular species of special

importance, either because those species can be used as ecological indicators for land use-related environmental changes or because those species can pose a threat to the environment under certain conditions of land use intensity. The central question is how to adopt sustainable agricultural practices in fragile arid and semi-arid savanna ecosystems. Using terrestrial small mammals—an important functional group within savanna ecosystems—as parameters of ecological stability or vulnerability, we aim to assess the sustainability of different agricultural practices (wildlife and livestock grazing, crop farming) in different areas of northern Namibia.

2. Materials and Methods

2.1. Study Region and Research Areas

The study region is situated in the dry bushland savanna of north-central Namibia and belongs to the Karstveld savanna biome [36]. The landscape is composed of a matrix of commercial farmland, which underwent a visible transformation process due to small-scale cropland expansion, increased grazing, altered fire frequency and land-use pressure [37]. However, these landscapes provide numerous border habitats with remnants of the original flora and associated important ecosystem goods and services. Most importantly, the fenced Etosha National Park is exerting an influence on the surrounding landscape at several spatial scales and different ecological levels [11,12,38].

Within this region, field research has been conducted in two different areas within the same homogenous eco-floristic and bioclimatic extent of the bushland savanna biome: (1) farmland adjacent to Etosha National Park (ENP) and (2) Tsumeb agricultural area. The farmland at the south-western border of the neighboring ENP (1) is administratively part of the Kunene region (19.563° S, 14.031° E), whereas Tsumeb agricultural area (2) is situated approx. 100 km from the eastern part of ENP in the Oshikoto region (19.2443° S, 17.7281° E). Both study areas lie on Karstveld, a massive deposit of calcrete and dolomites that represents the former remnant of Owambo basin folded upwards during the formation of ancient Gondwanaland. Two broad geological substrates mainly characterize the geological features and the soil characteristics: (1) loam-clay and (2) dolomite sands from the underlying rock formations [36]. Almost the entire study region comprising these two study areas can be characterized as arid to semi-arid savanna with 250–500 mm of average annual rainfall and a strong seasonality and high variability in years and timing. As is typical in this region, rainfall occurs during the summer months (between October and April) but more frequently peaking between February and April [36]. The region generally experiences a single dry season from May to November. The coolest months of the year are June and July with mean lowest night-time temperatures of 7 °C. The main vegetation consists of shrub and thornbush savanna characterized by the coexistence of woody and herbaceous communities with differing phenological cycles (diverse semi-deciduous tree species, partly open grassland). The dominant woody plants are *Colophospermum mopane* trees and shrubs, *Acacia* species, *Catophractes alexandrii*, *Terminalia prunioides* and *Combretum apiculatum* woodland. Some areas suffer considerable bush encroachment by *Dicrostachys cinerea*. The grass layer in these rangelands is dominated by palatable species, which provide important grazing resources for livestock and game animals in the area. On the other hand, dominant perennial and annual grass species such as *Anthephora pubescens*, *Digitaria eriantha*, *Cynodon dactylon*, *Cenchrus ciliaris*, *Aristida stipitata* and *Enneapogon cenchroides* are common.

Land use on farmland at the south-western border of the ENP ranges from classical livestock farming to game farming in the form of eco-tourism, game meat production and/or trophy hunting. Major parts of the farmland are fenced, leading to locally high herbivore densities. Moreover, the creation of artificial watering points results in high populations and locally large aggregations of various herbivorous species, such as *Tragelaphus strepsiceros*, *Phacochoerus africanus*, *Oryx gazella*, *Tragelaphus oryx*, *Antidorcas marsupialis*, *Equus zebra hartmannae* and *Connochaetes taurinus*, so that there is a high grazing pressure by wild ungulates around the vicinity of available water [39]. Due to the fertile nature of the soil, the area around Tsumeb is one of the most important agricultural farming areas, dominated

by several commercial small- and large-scale farming systems such as commercial livestock ranching, game farming, tourism and mixed cropping production (maize, lucerne, cotton and vegetables) under irrigation.

2.2. Farm Management Practices and Site Selections

The study region comprises a mosaic of arable farmland, cattle grazing farmland and semi-natural farmland. Data from private farmland bordering the ENP were collected at one site each of the following habitat types along a gradient of increasing land use intensity: near natural wildlife rangeland (WF1), wildlife rangeland close to an artificial waterhole (WF2), and livestock rangeland grazed by cattle (C) (Figures 1 and 2). Within the Tsumeb agricultural area, we selected two sites each on smallholder farmland representing the following land use types: livestock rangeland with encroaching bushland (EBL) and cleared bushland (CBL), and arable land with maize fields (MF), and lucerne fields (LF) (Figures 1 and 2). Three classes of land use intensity were distinguished in each study area: low, medium, and high. The definition of each class was based on the type of land use and the degree of anthropogenic transformation. The remote rangelands in the near-natural savanna ecosystem of the Etosha area were considered as areas with a low degree of anthropogenic transformation, whereas the populated rangelands and irrigated croplands of the Tsumeb area were considered as areas with a high degree of anthropogenic transformation. Based on this first classification, land use intensity in the Etosha area was considered as ‘low’ in the absence of any management, as ‘medium’ in the vicinity of an artificial waterhole with a high concentration of grazing wild ungulates, and as ‘high’ on the cattle grazing area. Land use intensity in the Tsumeb area was considered as ‘low’ within non-managed (bush encroached) cattle grazed rangelands, as ‘medium’ within cleared bushlands and as ‘high’ within irrigated arable monocultures. To minimize the influence of other environmental factors (e.g., micro-climate, soil properties), the sampling sites within the respective study areas were carefully selected to have similar topographic and soil characteristics.

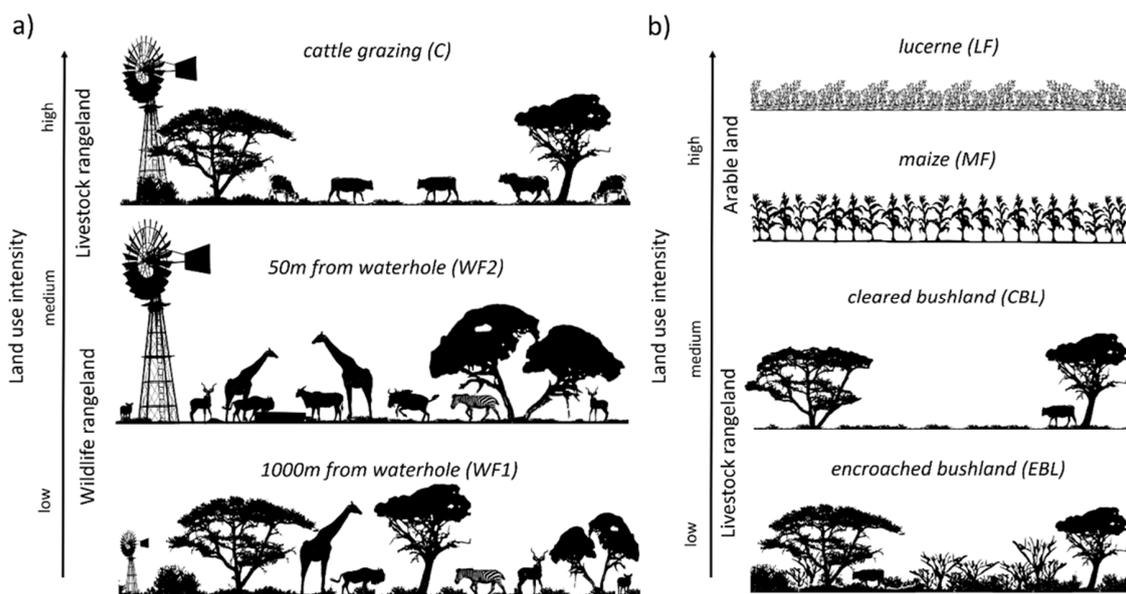


Figure 1. Study design: small mammal communities were investigated in three different habitat types (wildlife rangeland, livestock rangeland, arable land) with different land use intensities (‘low’, ‘medium’, ‘high’) on (a) private farmland south of ENP (low anthropogenic transformation) and (b) smallholder farmland in Tsumeb agricultural area (high anthropogenic transformation).



Figure 2. Location of the study areas (red circles in overview map) and sampling sites (yellow diamonds) in Namibia: (1) left—at the southern boundary of ENP near the city of Kamanjab and (2) right—around the city of Tsumeb; WF1/ WF2 = wildlife rangeland, wildlife rangeland in 1000 m/50 m distance to waterhole; C = livestock rangeland grazed by cattle; EBL/ CBL = encroached bushland/cleared bushland, MF/ LF = maize/lucerne field.

2.3. Small Mammal Sampling

Small mammals were trapped using 100 (farmland south of ENP) and 90 (Tsumeb area) Sherman standard live traps, respectively, on each site spaced at 10 m intervals arranged in rows with 10 traps per row within a trapping quadrat (grid). In order to minimize patchiness and possible fragmentation of the study sites (to avoid the grid spanning over several habitat types) and enable obtaining habitat-specific estimates, specific site selection for grid establishment was based on prior subjective assessment. Traps were baited with a mixture of peanut butter, water and oats following Hoffmann and Zeller [27] and checked every morning. In each study, we performed trapping sessions for 4 consecutive nights [40,41]. In the Etosha area, we conducted four trapping sessions per study site from July to November in 2006 (4800 trap nights). In the Tsumeb agricultural area, we conducted two trapping sessions per study site in March 2017, Nov 2017, February 2018, May 2018, and December 2018 (3570 trap nights). Handling of captured animals was done in accordance with the Guidelines from the American Society of Mammalogists [42]. Animals were carefully removed from the live trap into a tube of acrylic glass for short-term immobilization for identification. Several external characteristics and measurements were used for species identification including shape of the body, weight, color, fur patterns, total length, tail length, ear length, right hind foot length. Small mammal species that could not be identified at the species level were identified at the genus level. After species identification, captured animals were released at the point of capture. Furthermore, voucher specimens of questionable individuals were retained as a reference for further taxonomic identification at the National Museum of Namibia. During the study conducted in the Etosha area, captured animals were colour-marked to identify recaptured individuals in order to estimate species abundance, diversity, and evenness.

2.4. Data Analysis

To understand how small mammal communities change across land use types and management practices, we estimated different community parameters: species richness (S) was defined as the total number of species captured per study site. Diversity was calculated using the Shannon diversity index

($H = -\sum p_i \times \ln(p_i)$, where p_i represents the proportion of individuals from species 'i' [43]) with the software PAST [44]. Shannon's equitability (E_H) was calculated to measure the evenness of small mammal communities ($E_H = H/H_{\max} = H/\ln S$).

The relative abundance of species captured in the Etosha area was assessed using the total number of captured individuals (excluding recaptures) divided by the number of trap nights. Data were converted to individuals per 100 trap nights [45,46]. We compared this index of relative abundance with a catch-effort index, the relative capture index (RCI), which gives the frequency of captures per trap per night. This index is a simple comparative trapping frequency index that can be used as an alternative to the relative abundance [47,48]. We calculated the RCI for each species as the number of captures divided by the total number of trap nights and converted this as per 100 trap nights to facilitate comparisons among habitat types within and between the two study areas, Etosha and Tsumeb. In order to validate the use of this index as an indirect measure of relative abundance, we compared the RCI with the relative abundance index from the Etosha data and performed a Spearman-rank correlation to assess the relationship between relative abundance and RCI. There was a strong positive correlation between relative abundance and the RCI, which was statistically significant ($r_s = 0.97$, $df = 16$ $p < 0.001$, $z = 0.472_{0.05}$, Figure S1), suggesting that the RCI can be used as a valid proxy for the relative abundance of small mammals. For this reason and in order to compare the data from both study areas, we refer to the RCI as an indirect measure of relative abundance in the further course of the manuscript. Furthermore, the relationship between ecological parameters RCI and S was investigated by plotting the total values of the calculated RCI and species richness (total number of species summed over all sample nights) for each site using Microsoft Excel. As the study design implies repeated measures, we controlled for experimental variability and evaluated temporal and spatial effects on mean RCI and S using one-way ANOVA (Geißer-Greenhouse correction), a Friedman test, a two-sample t-Test or a two-sample Kolmogorov–Smirnov (K–S) test, depending on the type and distribution of the data. Data were tested for normality (Shapiro–Wilk test) and homogeneity of variance (Levene's Test). The minimum level of significance for all tests was 0.05. We conducted all statistical tests using GraphPadPrism version 9.0.0 for Windows (GraphPad Software, La Jolla, CA, USA, www.graphpad.com)

3. Results

3.1. Etosha Area

We captured nine species in total in the Etosha area, of which three were captured on all three study sites: *Micaelamys namaquensis* (Smith, 1834), *Elephantulus intufi* (Smith, 1836) and *Gerbilliscus leucogaster* (Peters, 1852) (Table 1). Whereas the RCI and species diversity were similar on the two wildlife rangeland sites, reduced values of these parameters were recorded on livestock farmland (Table 1 and Table S1). Species richness (S) was highest at the site with medium land use intensity (wildlife rangeland site close to the waterhole; $S_{WF2} = 9$) and similar between the two other sites (low and high land use intensity; $S_{WF1} = 4$ and $S_C = 5$). Except for site WF2 (medium land use intensity), there was no statistically significant effect of time (variability between trapping sessions) on mean RCI or S (Table S2). On site WF2, mean RCI and species richness were significantly lower during the first trapping session, compared to the mean RCI and species richness of the following three trapping sessions.

Table 1. Summary of trapping data (total number of captures per species across all trapping sessions) from study sites on private farmland at the southern Etosha boundary; changes in species' capture frequency of $\geq 50\%$ between classes of land use intensity are highlighted in bold. RCI—relative capture index based on number of captures per 100 trap nights. WF1/WF2—near-natural wildlife rangeland/wildlife rangeland close to artificial waterhole, C—cattle farm.

	Wildlife Rangeland				Livestock Rangeland	
	WF1		WF2		C	
	low		medium		high	
land use intensity	1600		1600		1600	
trap nights	1600		1600		1600	
species	captures	RCI	captures	RCI	captures	RCI
<i>Crocidura</i> sp.			1	0.062		
<i>Dendromus melanotis</i>			1	0.062		
<i>Elephantulus intufi</i>	25	1.56	50	3.12	26	1.63
<i>Gerbilliscus leucogaster</i>	245	15.31	148	9.25	1	0.06
<i>Micaelamys namaquensis</i>	284	17.75	23	1.44	174	10.88
<i>Mus indutus</i>	195	12.19	455	28.44	34	2.125
<i>Saccostomus campestris</i>			1	0.06		
<i>Steatomys parvus</i>	4	0.25	41	2.56		
<i>Thallomys nigricauda</i>			1	0.06		
total	753	47.06	721	45.06	235	14.69

Moreover, we detected species-specific response patterns to land use intensity: the RCI of *G. leucogaster* continuously decreased from low land use intensity (non-disturbed wildlife rangeland) to high land use intensity (livestock farmland), where this species was captured only once. In contrast, the RCI of *Mus indutus* (Thomas, 1910) increased from low land use intensity (non-disturbed wildlife rangeland) to medium land use intensity (wildlife rangeland close to the waterhole). On livestock farmland, however, *M. indutus* revealed a reduced RCI. Likewise, *E. intufi* showed a similar pattern but the decrease in the RCI on livestock farmland was not as pronounced as for *M. indutus*. *M. namaquensis* was most abundant on non-disturbed wildlife rangeland. With medium land use intensity, we observed a decrease in the RCI of this species, however, followed by a tenfold increase with high land use intensity.

3.2. Tsumeb Area

Out of eight species captured in the Tsumeb area, the three species *Mastomys natalensis* (Smith, 1834), *Aethomys crysophilus* (de Winton, 1897) and *G. leucogaster* were represented across all investigated habitat types (Table 2). *M. natalensis* was the dominant species across all but one trapping site. The remaining five species were exclusively associated with bushland but not with arable land. *Dendromus melanotis* (Smith, 1834) and *Crocidura* sp. have been captured only once. Species richness and community composition were comparable between sites with low and medium land use intensity, while capture frequency strongly decreased. In contrast, species richness decreased from medium to high land use intensity (transition from livestock rangeland to arable land), while overall capture frequency strongly increased. Except for the habitat type EBL (low land use intensity), there was no statistically significant effect of time (variability between trapping sessions) or landscape (variability between sites) on mean RCIs or mean species richness (Table S3). On encroached bushland, a significant difference in the mean RCI between the trapping sessions of site 1 was determined (February 2018 and December 2018, Table S3).

Table 2. Summary of trapping data (total number of captures per species across all trapping sessions) from study sites in Tsumeb agricultural area; changes in species' capture frequency of $\geq 50\%$ between classes of land use intensity are highlighted in bold; RCI—relative capture index based on number of captures per 100 trap nights. EBL/CBL = encroached/cleared bushland; MF/LF = maize/lucerne field.

	Livestock Rangeland				Arable Land			
	EBL		CBL		MF		LF	
land use intensity	low		medium		high		high	
trap nights	990		990		630		960	
species	captures	RCI	captures	RCI	captures	RCI	captures	RCI
<i>Aethomys crysophilus</i>	26	2.62	7	0.71	61	9.68	138	14.38
<i>Crocidura</i> sp.	2	0.2						
<i>Dendromus melanotis</i>					1	0.16		
<i>Elephantulus intufi</i>	8	0.81	3	0.3				
<i>Gerbilliscus leucogaster</i>	180	18.18	17	1.71	18	2.86	20	2.08
<i>Mastomys natalensis</i>	150	15.15	94	9.49	253	40.15	272	28.34
<i>Mus</i> sp.			8	0.8				
<i>Steatomys pratensis</i>	18	1.82	18	1.82				
indet.	24		21					
total	408	41.21	168	16.96	333	52.85	430	44.79

The response patterns of *M. natalensis* and *A. crysophilus* to land use intensity seemed similar: in both species, the RCI was lower on cleared bushland (medium land use intensity) compared to encroached bushland (low land use intensity) but increased on the arable land sites (high land use intensity). However, while for *M. natalensis* the RCI was about twice as high on the maize fields compared to lucerne fields, the RCI of *A. crysophilus* showed a threefold increase from maize to lucerne.

3.3. Cross-Area Comparison

The results point towards different patterns of small mammal responses to land use intensity in the two study areas (Figure 3). In the comparatively less disturbed Etosha area, species richness increased with medium land use intensity, while overall capture frequency remained constant. However, at the transition from wildlife rangeland to livestock rangeland (from medium to high land use intensity), a reduced capture frequency and a decrease in species richness to the initial level was observed. In the agriculturally heavily influenced Tsumeb area, on the other hand, there was initially no change in the number of species with increasing land use intensity, although a measurable reduction in small mammal capture frequency was observed on cleared bushland. With continuing land use intensity—at the transition from livestock rangeland to arable land—species richness declined, coupled with a marked increase in overall capture frequency.

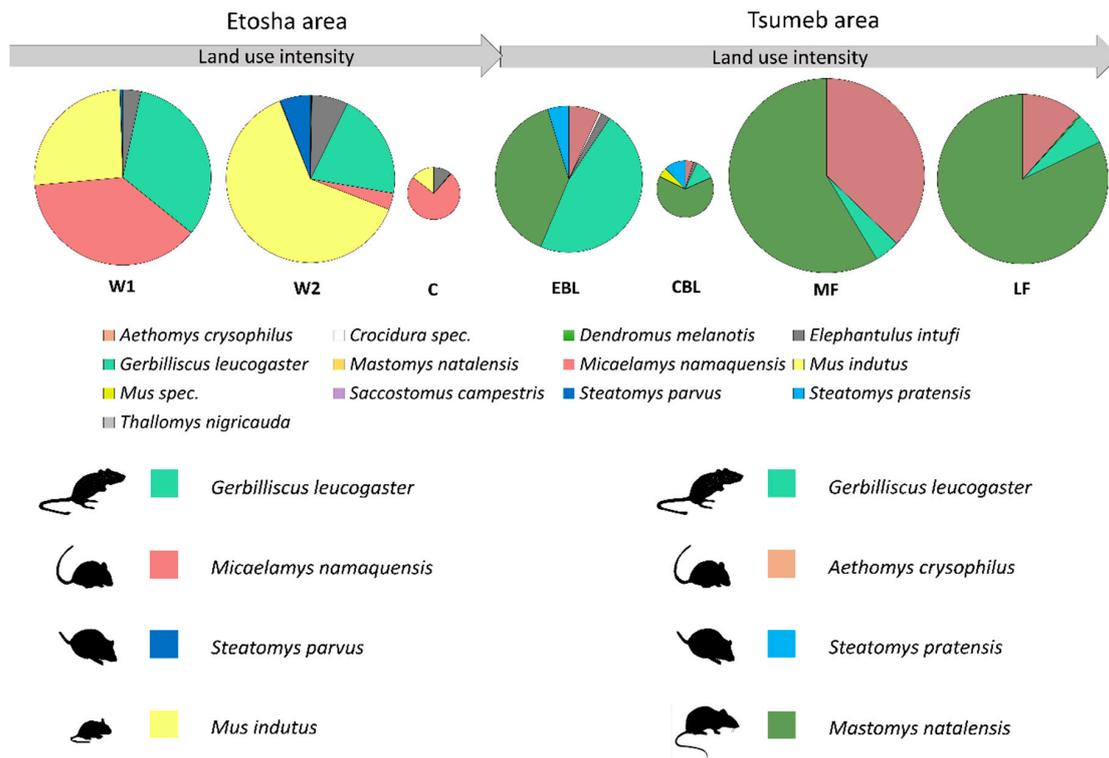


Figure 3. Species composition and capture frequency (RCI-captures/100 trap nights) along two gradients of land use intensity in the two study areas. Size of pie charts relates to total RCI values. WF1/WF2 = wildlife farmland 1000 m/50 m distance from waterhole, C = cattle farm, EBL/CBL = cattle grazing on encroached/cleared bushland; MF/LF = maize/ lucerne field. Species responding with changes in capture frequency of $\geq 50\%$ between classes of land use intensity are shown below (*G. leucogaster*, *M. namaquensis*, *A. crysophilus*, *S. parvus*, *S. pratensis*, *M. indutus*, *M. natalensis*).

Moreover, the relationship between the ecological parameters (relative capture index [RCI] and species richness [S]) and the intensity of land use in the two study areas was examined (Figure 4). In the less transformed area (Etosha area), increasing land use intensity led to a clear decrease in the RCI. In contrast, increasing land use intensity in the more transformed area (Tsumeb area) first led to a decrease in capture frequency, followed by a clear increase on the arable land sites. In the Etosha area, medium land use intensity (concentrated grazing by wild ungulates close to waterhole) first led to an increase and the highest overall value of measured species richness ($S = 9$), while further increasing land use intensity (cattle grazing) resulted in a decreased number of species ($S = 4$) comparable to the number of the site with low land use intensity ($S = 5$). Species richness on bushland sites in the highly transformed agricultural area of Tsumeb was slightly higher compared to bushland in the near-natural savanna ecosystem of the Etosha area but was clearly reduced from $S = 6$ to $S = 3$ with increasing land use intensity at the transition from cleared bushland to arable farmland (Figure 4).

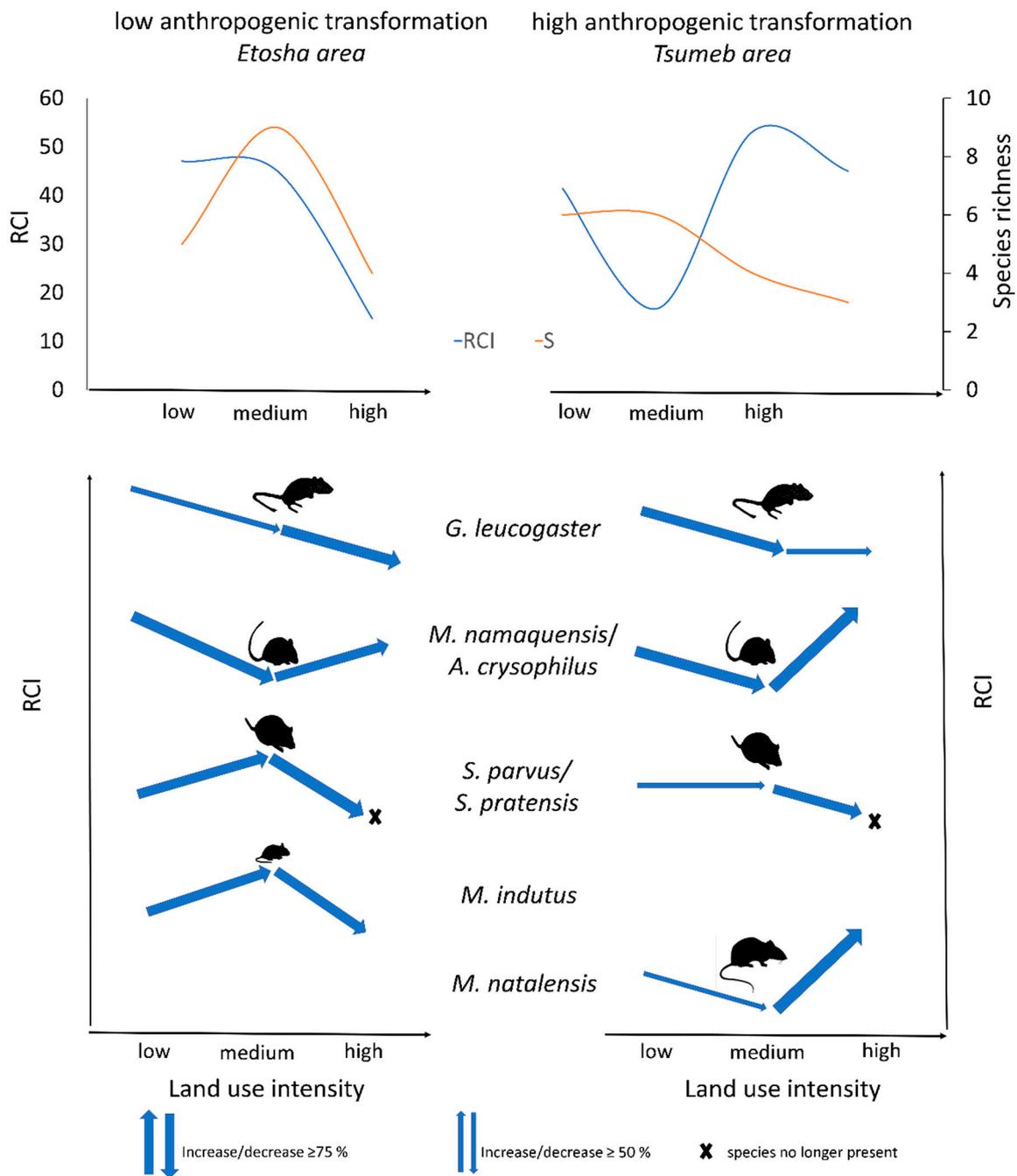


Figure 4. Relationship between ecological parameters (total values of RCI and S) and schematic representation of response patterns of different small mammal species along gradients of land use intensity (low, medium, high) in the two study areas with different degrees of anthropogenic transformation (Etosha area, Tsumeb area).

4. Discussion

In this study, we investigate and compare the response patterns of small mammal communities to increasing land use intensity in two distinct areas in Namibia (Etosha vs. Tsumeb). Within each area, small mammal communities respond towards increasing land use intensity through changes in species richness and the relative capture index (RCI). After accounting for experimental variability and the effects of time and local landscape, we come to realize that the respective response pattern, however, differs between the two areas: in the Etosha area, a change from low to medium land use intensity

is associated with an increase in species richness, while the overall RCI remains on a similar level. With the transition from medium to high land use intensity, species richness almost resembles the initial (low-intensity) value, while the overall RCI decreases. In the Tsumeb area, by contrast, a change from low to medium land use intensity does not affect species richness but leads to a decrease in the overall RCI. With the transition from medium to high land use intensity, the species richness in Tsumeb area decreases, while the overall RCI increases (Figure 4).

To understand these different response patterns, we have to consider the degree of landscape transformation, as well as the nature of land use change within the respective areas. In the Etosha area, the area of low land use intensity represents a relatively undisturbed savanna ecosystem—a wildlife farm bordering Etosha National Park in Namibia. As shown by Rottstock et al. [49], such wildlife farms can be regarded as examples of relatively undisturbed savanna systems. The transition from low to medium land use intensity results from increasing grazing pressure in close proximity to a waterhole (Figure 1). The increase in small mammal species richness corresponds to the concept of the Intermediate Disturbance Hypothesis [50]. Accordingly, a community's species richness initially increases when an undisturbed system is exposed to a moderate degree of disturbance. Further increasing the degree of disturbance, however, will lead to a decrease in species richness. In our study, accumulated wildlife grazing close to a waterhole induced a moderate disturbance that obviously enhanced structural complexity of the habitat and contributed to an increase in the species richness of the small mammal community. This effect became pronounced as the dry season progressed (Table S2): mean RCI and species richness were significantly higher during the trapping sessions 2–4 (Sept–Nov) compared to the first trapping session (July). In fact, this finding actually underlines the underlying biological effect of an increased species number resulting from medium land use intensity (WF2) when compared to low land use intensity (WF1): in the course of the dry season, the grazing pressure induced by increasing numbers of wildlife in the immediate vicinity of the waterhole apparently increased the disturbance in the course of our trapping sessions. The decrease in the overall RCI of the small mammal community under high land use intensity appears to be a result from an increased grazing pressure from livestock (Figures 3 and 4). This increased grazing pressure is accompanied by a reduction in the structural complexity (decrease in the degree of vegetation cover, soil compaction) and consequently the quality of the small mammal habitat.

This relationship between increasing grazing pressure and decreasing overall abundance of small mammal communities has been described in several previous studies [51–55]. The program BIOTA, a study in the Nama Karoo, clearly demonstrated that high grazing pressure significantly reduces the structural complexity of the habitat (vegetation cover and composition), and thus acts as a disruptive factor for small mammals [27,29]. Similar observations in a thornbush savanna area in Otjomongombe or in south-eastern Kalahari Sandveld of Namibia's Omaheke Region (also within the BIOTA programme) support these findings: the authors showed that the abundance of small mammal communities on managed farmland is strongly positively correlated to vegetation cover [28,55]. Likewise, a study at Waterberg Plateau Park in Namibia confirms a decline in overall abundance of small mammal communities resulting from increasing grazing pressure [56]. Grazing can alter the structure and functions of grassland systems in many ways. In general, grazing leads to the removal of plant biomass and a decrease in vegetation height or coverage [57,58]. Moreover, selective feeding and trampling, especially by cattle, can change the abundance of different plant species and alter the composition and diversity of local plant communities [59,60]. Such alteration in vegetation structure can have pronounced impacts on small mammal communities, since it affects the availability of food and cover [61,62].

The above-mentioned studies consider the effect of increasing grazing pressure on small mammal communities. The situation in the Tsumeb area is different. Here, the increasing land use intensity results from the conversion of bushland to uniform and homogenous arable land. Unlike in the Etosha area, the initial situation in the Tsumeb area (bushland) does not represent a relatively natural system. Instead, the bushland habitat in the Tsumeb area is already the result of an anthropogenic-induced

transformation process. Accordingly, our study sites in the Tsumeb area are characterized by a higher degree of transformation when compared to the study sites in the Etosha area. Not surprisingly, the overall RCI of the small mammal community on the cleared area is lower compared to the community on the bushland site, as the cleared area featured a lower level of structural complexity of the habitat. However, the species richness appears not affected by the clearing of bushland. In some way, this finding needs to be considered with care as there seems to be great variability between the trapping sessions on one of the two bushland sites (Table S3). However, a more important effect actually emerged at the transition from cleared bushland to arable land, namely the increase in the overall RCI and the decrease in species richness (Figures 3 and 4). This result was unaffected by effects of time or local landscape (Table S3). In the Tsumeb area, livestock production is continuously replaced by irrigation-based crop farming, involving the preparation of land through clearing of bushland. However, woody vegetation is an integral component of savannas and its removal implies a decrease in structural complexity. The transition from intermediate to high land use intensity—the conversion of cleared bushland into maize or lucerne fields—goes along with a reduction in structural complexity and floristic diversity of the habitat [63]. At this transition to arable land, we observed a decline in small mammal species richness, while the overall RCI increased substantially. Thus, it can be assumed that the structural homogeneity and uniformity of arable land leads to a break-up of a relatively complex small mammal community, but provides favorable living conditions for the remaining species (i.e., *M. natalensis* and *A. crysophilus*), which occur in very high densities (see below).

Regardless of the different relationships between species richness and the RCI in the two areas (Figure 4), particular species within these communities show similar response patterns and it seems reasonable to take a closer look at the mechanisms behind these responses. The bushveld gerbil (*G. leucogaster*) is the only species that occurs in both areas and that also responds in both areas in a similar way: increasing land use intensity leads to a significantly decreasing RCI. In contrast with several other species, *G. leucogaster* does not benefit from the moderate disturbance in the Etosha area (medium-intensity site). Rather, the RCI constantly decreases with increasing land use intensity. It seems that the beneficial effects resulting from changes in structural complexity of the vegetation cannot outweigh negative effects associated with an increase in grazing pressure. Grazing pressure can lead to alteration of the soil and the sensitivity of *G. leucogaster* to increasing grazing pressure seems related to soil compaction. As a species that excavates complex burrow systems, *G. leucogaster* prefers deep and light sandy soils [64,65] (Table S4). Apparently, the decreased RCI of *G. leucogaster*—both under increasing grazing pressure in the Etosha area and under habitat conversion to monoculture cropland in the Tsumeb area—results from changes to the soil. Our results suggest that *G. leucogaster* can be used as an ecological indicator of ecosystem integrity and the condition of savanna landscapes. This assumption was already made by other authors [27,56]. Based on our data, we can confirm the validity of this proposed indicator species. *G. leucogaster* actually meets all suitability criteria that a useful indicator species should have, as defined by McGeoch: (a) a broad distribution range, (b) a specialization to clearly defined habitat requirements (in this case light and sandy soils), (c) easy taxonomic identification, (d) distinctive sensitivity to a specific environmental change (in this case soil degradation), (e) cost effectiveness, and (f) its response to a specific environmental change should resemble the response of other species [66]. It is important to note that the response towards soil compaction is linked with bioturbation [10] but also reproduction, since especially altricial species with prolonged lactation strongly depend on sufficient soil conditions to successfully reproduce under harsh environmental conditions [67] (Table S4).

Besides *G. leucogaster* showing a similar response pattern in both areas, certain vicarious species also respond in a similar way to increasing land use intensity. Interestingly, the low-intensity sites in both areas feature a species of fat mice—*Steatomys parvus* Rhoads, 1896 in the Etosha area and *Steatomys pratensis* Peters, 1846 in the Tsumeb area. Both *S. parvus* and *S. pratensis* disappear with high land use intensity. Fat mice are known for their strategy to increase their survival in times of limited food availability by storing fat [64,68,69]. This adaptation to changing food availability already implies a

high sensitivity to changing environmental conditions. Similar to *G. leucogaster*, fat mice also depend on deep, sandy soils in order to construct deep burrows with several tunnels in which they can enter the torpor in times of limited food availability [64,70–72] (Table S4). Changes in food availability and soil degradation due to pasture (*S. parvus*) or monoculture (*S. pratensis*) seem to prevent these species from continuing their energy-saving survival strategy.

Another similarity between the communities in the two areas exists in view of *M. namaquensis* (Etosha area) and *A. crysophilus* (Tsumeb area). These species have a close phylogenetic relation, and *M. namaquensis* was officially listed under the name *Aethomys namaquensis* (Smith, 1834) until a few years ago [73,74]. Both species show a rat-like appearance and share similar ecological adaptations with regard to reproduction and nutrition (Table S4). They are comparatively flexible in their habitat requirements and, in the event of severe disturbance, can apparently benefit from the disappearance of other species and become dominant species of the respective community owing to the lack of interspecific competition [64,75,76]. Both species, but especially *A. crysophilus*, tend to have explosive population growths due to their reproductive biology (year-round, short gestational period) [75,76]. Moreover, these species can make use of already existing burrows and are not dependent on particular soil conditions, as is the case for the bushveld gerbil or fat mice (see above) [73,74].

In addition to these three examples of similar response patterns of species within the two communities, we also observed area-specific response patterns of particular species. In the Etosha area, this is the case of *M. indutus*. In contrast to the bushveld gerbil (see above), *M. indutus* obviously benefits from the change in habitat heterogeneity associated with a moderate degree of disturbance. With a high degree of disturbance, however, the RCI of *M. indutus* significantly decreases. This is not surprising, since *M. indutus* tends to avoid open habitats [64] and would be forced to cover long distances without shelter from vegetation on the high-intensity site (cattle farm). However, the decreased RCI on the cattle farm might also be a result of the reduced availability of grasses, as *M. indutus* depends on a sufficient grass layer to construct grass nests in shallow burrows for reproduction (Table S4) [64]. In the Tsumeb area, an important response pattern was found for *M. natalensis*. This species shows a remarkable increase in the RCI on arable land, where it becomes the dominant species. *M. natalensis* is the most widespread rodent species in Africa and colonizes a variety of different habitats [77,78]. Its broad distribution range already indicates a wide ecological plasticity and underlines the role of *M. natalensis* as a pioneer species in the colonization of areas following agricultural (over-)utilization [79]. It is known that favorable environmental conditions (e.g., extended rainfall, phytohormones of sprouting vegetation) can trigger the reproductive activity in *M. natalensis* [80–82] (Table S4). Not surprisingly, *M. natalensis* can displace and outcompete other species [81]. Consequently, we found the decreasing RCI of *G. leucogaster* to be coupled with an increasing RCI of *M. natalensis*. This finding is supported by observations in Waterberg Plateau Park [56]. The competitive advantage of *M. natalensis* is linked with the species' life history, particularly its reproductive strategy. As a highly r-selected species, *M. natalensis* populations can exceed high numbers within a short period of time [79]. Its reproductive strategy is characterized by a high litter size (11–13 young/litter) in combination with a high number of litters per year (up to four litters), a short interval between litters, and a relatively early age at which breeding starts [80]. Furthermore, *M. natalensis* is a distinct food opportunist that feeds on what is available, but prefers seeds and cereals [79]. Therefore, irrigation-based cropping systems may particularly increase the resources available for *M. natalensis* and it seems reasonable that several generations of this species can survive in a newly established agricultural system. The explosive population growth of this species can be problematic, since it is involved in damages to a large number of cereal crops in southern Africa [81,83] and is considered a main reservoir for important zoonoses such as Lassa virus, Lyme disease, or plague. However, despite its occurrence throughout Southern Africa, *M. natalensis* has not been captured in the Etosha area. One reason could be that this species nowadays is almost always found in close association with humans in rural villages and surrounding cultivated fields and, less commonly, in sparsely populated grasslands [83]. In addition, Happold and

Happold [84] demonstrated that the abundance of *M. natalensis* may be extremely patchy, with large numbers occurring in preferred habitats and almost no individuals in nearby habitats.

5. Conclusions

Our study reveals different response patterns of small mammal communities to increasing land use intensity in two distinct areas (Etosha area vs. Tsumeb area). Within the less-transformed Etosha area, the species richness remains relatively constant and small mammal communities respond to increasing land use intensity by shifts in species composition. This shift in species composition may already result in the weakening of some ecosystem functions such as bioturbation, seed dispersal and food supply for predators. The change in the overall RCI has the potential to further weakening these functions. Within the more-transformed Tsumeb area, the species richness decreases substantially, while the RCI of a few species increases dramatically. The conversion of bushland into irrigated arable land results in a break-up of a balanced small mammal community and the unhindered rise of a few pest species. Obviously, these different response patterns are linked with an area's degree of landscape transformation, the nature of land use change, as well as the ecological adaptations of involved species [85]. *Gerbilliscus leucogaster* shows a distinctive sensitivity to land use-related soil degradation in both areas, suggesting that this soil-dwelling species can be used as an ecological indicator of ecosystem integrity and the condition of savanna landscapes. *Mastomys natalensis* has the potential to become an important pest species when bushland is transformed into irrigated arable land. Our results highlight the importance of area-specific management measures for biodiversity conservation in savanna ecosystems. Given the role of small mammal communities in agricultural ecosystems, the maintenance of species richness and a balanced community structure is of great importance to protect biodiversity and to reduce the risk of uncontrolled population growth of pest species.

Supplementary Materials: The following are available online at <http://www.mdpi.com/1424-2818/12/12/488/s1>, Figure S1: Spearman correlation of relative abundance and relative capture index on the three study sites in the Etosha area. Table S1: Small mammals captured by species on private farmland at the southern Etosha boundary. Table S2: Effects of time (variability between trapping sessions) on RCI (mean \pm SEM) and S (mean \pm SEM) in the Etosha area. Table S3: Effects of time (variability between trapping sessions) and local landscape (variability between sites) on RCI (mean \pm SEM) and S (mean \pm SEM) in the Tsumeb area. Table S4: Comparison of selected biological and ecological traits of small mammal species captured in the study areas.

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