

Conversion of savannah habitats to small-scale agriculture affects grasshopper communities at Mt. Kilimanjaro, Tanzania

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Abstract About 20 % of the natural grasslands in Sub-Saharan Africa have been converted to cropland and 80 % of the converted area is managed by small-scale farmers. Despite the large contribution of small-scale subsistence farming to agricultural expansion in Sub-Saharan Africa only few studies investigated the effects on insect biodiversity. We studied the effects of the conversion of savannah to small-scale extensively managed ruderal areas and corn fields on grasshopper communities (Orthoptera: Caelifera). The study was conducted on the eastern slopes of Mount Kilimanjaro, Tanzania. Three plots per land use type were established and grasshoppers were repeatedly collected between September and December 2010 using standardized transect walk methods. In comparison to the natural savannah, cornfields exhibited lower numbers and densities of grasshopper species, while ruderal areas exhibited similar species richness. However, vegetation cover was the best predictor for species richness, with the number

of grasshopper species nearly doubling from plots with scarce vegetation to those with a dense grass cover. The composition of grasshopper communities differed between land use types and vegetation cover, with habitat generalists being scarce. Therefore, the species richness of all land use types combined was considerably higher than the richness of single land use types. We found no rare or threatened species during sampling. Our study suggests that a mosaic agricultural landscape with areas of savannah and extensively managed ruderal areas may maintain a high biodiversity of grasshoppers. However, the effectiveness of such mosaics is strongly dependent on extensive farm management practises which retain significant amounts of grass cover throughout the year.

Keywords Biodiversity · Land use change · Habitat management · Herbivores · Orthoptera · Tropical ecology

Introduction

In the last century the area of tropical grasslands and savannahs decreased by over 50 %; primarily due to the conversion to agricultural land (Millenium Ecosystem Assessment 2005). In Sub-Saharan Africa approximately 20 % of the former grasslands are used as cropland while large parts of the remaining grasslands are used for livestock grazing (UNDP, UNEP, Worldbank and WRI 2000). The majority of the cropland, about 80 %, is farmed by small-scale subsistence farmers (Nagayets 2005; Havemann and Muccione 2011). In consideration of a growing human population the Food and Agriculture Organisation of the United Nations predicts a further expansion of small-scale subsistence agriculture into former natural grassland areas (Zhou 2011), with potential negative consequences

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for biodiversity and ecosystem function (Altieri 1999). Despite this acceleration of the conversion of natural habitats to arable land, little work is done on the effects of grassland conversion to agricultural land on insects in Sub-Saharan Africa.

Grasshoppers are among the most important herbivores in grasslands all over the world (Samways 1994; Branson et al. 2006) and account for a high percentage of arthropod biomass in these ecosystems (Gillon 1983). Furthermore, they serve as food for vertebrates, play a huge role in transporting and generating nutrients (Gandar 1980) and are major players in energy flow (Samways 1997; Belovsky 2000). Some species are even regarded as ecosystem keystone species (Joern and Gains 1990; Quinn et al. 1993). Grasshoppers are highly sensitive to changes in environmental conditions (Samways and Sergeev 1997), e.g. through grazing (Miller and Onsager 1991; Chambers and Samways 1998), fire (Gillon 1972; Bock and Bock 1991; Joern and Laws 2013) or land conversion (Kemp 1992). Thus, they have been used as indicators of habitat disturbance (Lockwood 1997; Anderson et al. 2001). Most studies which investigated the influence of land conversion on grasshoppers focused on the effects of grassland management especially by livestock grazing (e.g. Gebeyehu and Samways 2003; Batáry et al. 2007; Branson and Sword 2010). Extensive management of grasslands may positively affect species richness and abundance (Kruess and Tschamntke 2002; Gebeyehu and Samways 2003; but see O'Neill et al. 2003; Batáry et al. 2007), possibly due to an increased habitat heterogeneity (i.e. vegetation structure, richness and abiotic conditions) (Gebeyehu and Samways 2003; Joern and Laws 2013). However, compared to ungrazed/natural areas extensively managed grasslands may differ in their species assemblages. In addition to habitat heterogeneity, the total productivity [=net primary production (NPP)] of an area may also influence the species richness of arthropods (Joern and Laws 2013). The species-abundance hypotheses states that areas with a higher NPP can support higher population sizes of species. In consequence, local extinction rates may be lowered leading to more co-existing species and higher species richness (Kaspari et al. 2004). However, in agricultural landscapes only a small fraction of the total NPP may be available as resources for insects as most of it is used by the human population (Haberl et al. 2007).

At the foothills of Mt. Kilimanjaro, Tanzania, we conducted a case study on the effects of small-scale subsistence farming on insect diversity using grasshoppers as the focal group and identify the major drivers of community change. Savannah ecosystems used to dominate the lower slopes of the Kilimanjaro. However, this area witnessed extensive population growth and land use changes over the last 100 years, leading to a decline of natural habitats by

39.5 % between 1973 and 2000 (Mbonile et al. 2003). We investigated the effects of land conversion from natural savannah over ruderal areas (fallow fields usually grazed by cattle and goats) to corn fields by small-scale subsistence farmers on short-horned grasshoppers (Orthoptera: Caelifera: Acridomorpha). The following questions were addressed: (1) How do local grasshopper communities respond to habitat conversion in terms of abundance, species richness and community dissimilarity; (2) Which are the most important environmental drivers of community change?

Materials and methods

Study area

The study was conducted in the colline savannah zone at Lake Chala and the surrounding agricultural land (700–1200 m a.s.l.) on the eastern slopes of Mount Kilimanjaro, Tanzania (2°45′–3°25′S, 37°00′–37°43′E). Mean annual temperature is approximately 24.1 °C (Appelhans et al. 2014) and the mean precipitation per year in this area is 600 mm (Hemp 2006) with a long rainy season from March to May and a short rainy season in November and December. The Lake Chala area represents one of the largest remaining savannah fragments at the foothills of Mt. Kilimanjaro in Tanzania. However, 10 km from Lake Chala the large Kenyan Tsavo-West National Park is situated which may serve as a source habitat for the grasshopper communities of the Lake Chala area. The area adjacent to the Lake Chala savannah is agricultural land, which is a mosaic of fields, ruderal areas and farms (Fig. 1). The land is cultivated by small-scale farmers, who live directly by their fields or in small villages nearby. There are normally one or two crop cycles per year depending on the amount of precipitation during the short rainy season. The ruderal areas are usually long-term fallow fields which are grazed extensively by cattle and goats.

In total, nine plots (three per land use type) were selected to ensure that the heterogeneity of each land use type (natural savannah, ruderal area and corn fields) was well represented. Each plot had an area of 250 m² and was situated at altitudes of between 940 and 1163 m a.s.l. The ruderal area and cornfield plots were interspersed while the natural savannah plots were more aggregated, as savannah habitat was restricted to one major protected site. However, the mean distance between plot centers was 1.2 km, with a minimum distance of 350 m (ruderal areas and corn fields) or 450 m (natural savannah) between plots of one land use type. We checked for spatial non-independence of data by calculating Moran's I values for residuals of linear models using the *correlog* function in the R package *ncf* (Bjornstad

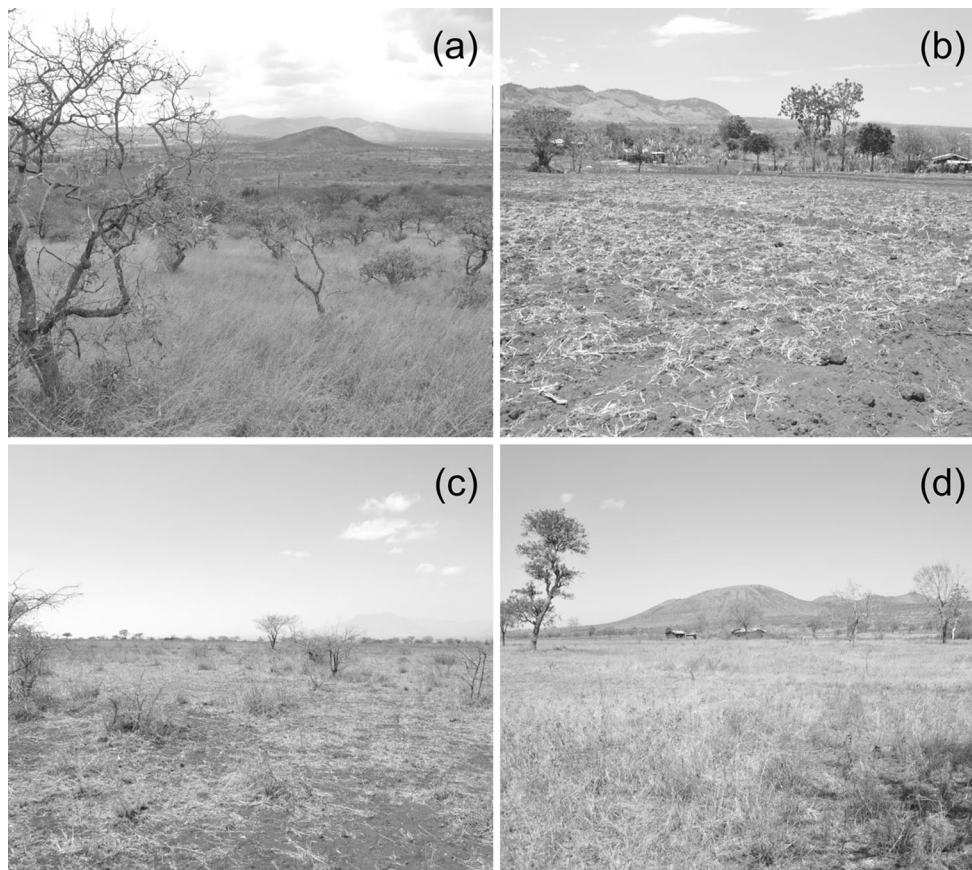


Fig. 1 Typical stand of **a** natural savannah, **b** corn field, **c** ruderal area with high grazing intensity and **d** ruderal area with low grazing intensity within the study area of the Lake Chala region at the eastern slopes of Mount Kilimanjaro, Tanzania

2013) and detected low, non-significant levels of spatial autocorrelation (Moran's $I < 0.293$, $p > 0.34$, Online Resource Table 1).

Grasshopper survey

Grasshoppers were sampled in six surveys using standardized transect walk methodology between 04th September and 04th December 2010. Each survey was 2–4 days long and each plot was sampled once within each survey. Sampling took place between 8:30 and 16:30 under similar climatic conditions, i.e. on days with low cloud cover and low wind speed, to avoid sampling bias due to heterogeneous weather conditions. Each plot was covered by twelve parallel transects, each being 50 m long and 4 m wide. The transects were paced slowly for 1 hour and adult grasshoppers spotted sitting on herbage and on the ground were collected with sweep nets or by hand and killed with cyanide. Large species with good flying abilities were mostly counted by sight. After collecting, all specimens were brought to the laboratory, identified to species level and counted. All grasshoppers collected in each 1 hour-

survey were pooled and used as subsample in the data analyses, resulting in six subsamples/surveys per plot.

Environmental variables

Grasshopper communities are known to respond more strongly to the structure than to the species composition of grasses (Gandar 1982; Hochkirch and Adorf 2007), so we examined the effect of vegetation structure rather than the effect of vegetation diversity on grasshopper communities. The vegetation structure on each plot was characterized in 16 equally distributed 1 m × 1 m squares. Each was subdivided into four units of 0.5 m × 0.5 m each, in which we measured the percentage of green grass, cragginess of the ground, vegetation cover on ground level, and grass height. Percentage of green grass was estimated at an ordinal scale (0–25 %: dry; 25–50 %: slightly green; 50–75 %: moderately green and 75–100 %: green). Cragginess of each unit was estimated at an ordinal scale (0: smooth; 1: slightly craggy; 2: moderately craggy; 3: craggy and 4: very craggy). Vegetation cover was estimated on a continuous scale between 0 and 100 % for each square. The height of

four haphazardly selected blades of grass per square, one in each unit, was measured to estimate the mean grass height. For each continuous parameter the mean of all 16 squares was used as a representative measure for the plot and for each ordinal parameter, the mode. Grass height was highly correlated with vegetation cover (Online Resource Table 2), thus we only used vegetation cover in statistical analyses which we interpret as an indicator of grass biomass.

Data analysis

All statistical analyses were conducted with R 2.12.1 (R Development Core Team 2011). To estimate the completeness of the species inventory of the three land use types, we calculated individual-based rarefaction curves for each land use type as well as the Chao, Jackknife 1 and Jackknife 2 species-richness estimator as recommended by Walther and Moore (2005). We used one-way analysis of variance (ANOVA) to test for differences in species richness and abundance among land use types. For this purpose, we first calculated the total species richness and abundance of each plot based on observed species richness and abundance of the six surveys. Species richness is the number of all species captured on the plot; abundance is the number of all individuals captured on the plot.

We calculated linear mixed-effect models (LME) for comparing the observed survey species richness among land use types with land use type as a fixed factor and plot as a random factor. The observed survey species richness is here defined as the number of species detected during one survey. We used the *lme* function from the *nlme* package (Pinheiro et al. 2011) for this purpose. When a post hoc test was necessary, we used the function *glht* from the *multcomp* package (Hothorn et al. 2008). The data were visually tested for normal distribution of errors and homogeneity of variance. When necessary, data were log-transformed to achieve a normal distribution of errors. To test the effects of the environmental structure variables on total abundance and species richness we used separated ANOVAs for the ordinal variables (cragginess, percentage of green grass) and linear regressions for continuous variables (vegetation cover). We calculated local false discovery rate values using the function *fdrtool* (package *fdrtool*; Strimmer 2008) to correct for multiple testing. Further, to estimate the relative support for each model containing one of the environmental variables or the land use type in predicting the species richness and abundance patterns we used the second-order Akaike information criteria (AICc) using the function *AICc* (package *MuMIn*; Barton 2012).

For all following calculations, we used the R package *vegan* (Oksanen et al. 2011). For the comparison of the

dissimilarity of species communities among different land use types, non-metric multidimensional scaling (NMDS) was applied using the function *metaMDS*. We used NMDS, because it can be used with any dissimilarity measure and it is more robust than a PCoA (Minchin 1987; Borcard et al. 2011). We calculated a NMDS-ordination on the total abundances per species per plot. Data were transformed using the Wisconsin double standardization. The Bray-Curtis-dissimilarity (function *vegdist*, method = bray) was used as distance measure because it has been found to perform well in ecological simulations (Faith et al. 1987). To test how structure variables influenced the composition of species communities we used the function *envfit*, which fits explanatory variables separately onto the ordination and tests their significance using permutation tests (999 permutations).

Results

Grasshopper survey

A total of 1398 individuals belonging to 40 species were captured. Of these, 20 species and 399 individuals were caught on corn fields, 24 species and 478 individuals in ruderal areas and 26 species and 521 individuals in natural savannah. With 367 individuals, *Rhaphotittha levis* was the most abundant species, followed by *Arcotylus meruensis* (219 individuals) and *Epacrocatantops curvicercus* (113 individuals). *R. levis* and *E. curvicercus* occurred in all land use types, but *E. curvicercus* was found equally in all land use types while *R. levis* was highly abundant in ruderal areas and natural savannah but rare in cornfields. *A. meruensis* occurred in cornfields and ruderal areas. Twelve species were captured only once (cornfields: 4, ruderal areas: 5, natural savannah: 3).

Rarefaction curves for each land use type as well as for all land use types combined did not attain a clear plateau, indicating that further species may probably be found with increased sampling effort. When comparing the observed species richness per land use type, corn fields showed a lower richness than ruderal areas and natural savannah. Natural savannah and ruderal areas had approximately the same species richness, although it was a little higher in natural savannah (Fig. 2). The richness estimators showed a similar pattern, whereas the Chao-index suggested higher species richness in ruderal areas than in natural savannahs. Comparing the number of observed species with the mean of the three estimators, all three land use types showed the same sampling completeness of 71–76 % (Table 1). When combining all samples from the three land use types the estimated species richness was

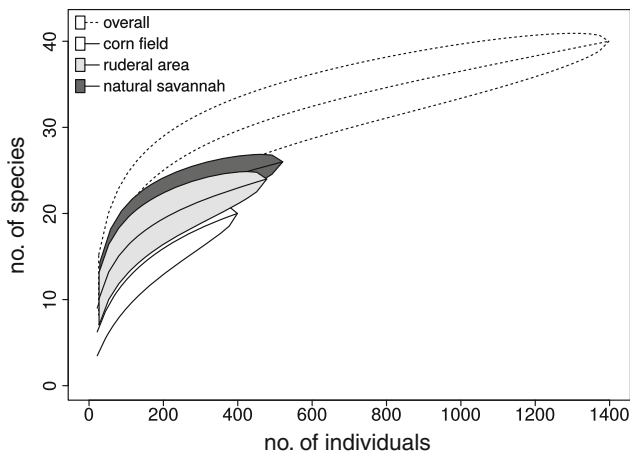


Fig. 2 Individual-based rarefaction curves for the three land use types and all land use types combined (overall) with 95 % CI

considerably higher than the richness of any single land use type (Table 1, Fig. 2).

The total number of species per plot showed a trend to differ among land use types (Table 2). The highest species richness was recorded in natural savannah (mean ± se: 17.33 ± 1.45) followed by ruderal areas (13.66 ± 1.45) and cornfields (11.33 ± 1.45) (Fig. 3). Observed survey species richness differed significantly among land use types (LME: $F_{2,6} = 5.57, p = 0.043$). Post-hoc tests indicated that there was a higher observed survey species richness in natural savannah than in cornfields (natural savannah—cornfields: z -value = 3.33, $p < 0.001$). No differences were found between ruderal areas and both other land use types (natural savannah—ruderal areas: z -value = -1.72 $p = 0.20$; ruderal areas—cornfields: z -value = 1.62 $p = 0.24$). Total

Table 2 Results of linear models testing for correlations of environmental variables and land use type with the abundance and species richness of grasshoppers

Variables	df	F value	p value	r ² value	AICc
<i>Abundance</i>					
Land use type	2.6	0.47	0.646	-0.153	111.05
Vegetation cover	1.7	2.38	0.167	0.146	102.53
% of green grass	1.7	0.61	0.460	-0.051	104.41
Cragginess	3.5	0.78	0.554	-0.090	120.91
<i>Species richness</i>					
Land use type	2.6	4.33	0.068	0.455	56.50
Vegetation cover	1.7	8.32	0.024*	0.478	50.30
% of green grass	1.7	7.08	0.032	0.432	51.06
Cragginess	3.5	3.05	0.130	0.435	67.17

Further, second-order Akaike information criteria values (AICc) for each model and adjusted r² values are given. Significant p-values are indicated by bold font. p values marked with asterisk (*) are significant after correction for multiple testing (false discovery rate)

abundances per plot did not significantly differ among land use types (Table 2). However, the highest abundance was recorded in natural savannah (173.66 ± 17.63) followed by ruderal areas (159.33 ± 33.15) and corn fields (133 ± 35.79) (Fig. 3).

Species richness correlated significantly with vegetation cover (Fig. 4) and less strongly with the percentage of green grass or the cragginess of the soil (Table 2). The total abundance of grasshoppers was not significantly correlated to any structure variable. For abundance and species richness the models including vegetation cover or percentage of green grass were better supported than the model which included land use type (Table 2).

Table 1 Estimated species richness (Chao-Index, Jackknife 1 and Jackknife 2) for all land use type combined (overall) and separated (CF = corn fields, RA = ruderal area, NS = natural savannah) as well as for each plot

Land use type	Obs. species	Chao	Jack1	Jack2	Obs. individ.	Complete (%)
<i>Overall</i>	40	112	51.78	62.39	1398	53
<i>CF</i>	20	26	25.67	28.49	399	75
CF 1	14	23	19	21.93	202	66
CF 2	11	11.5	12.67	11.87	115	92
CF 3	9	13.5	11.5	12.97	82	72
<i>RA</i>	24	36.25	30.61	35.16	478	71
RA 1	16	24.17	21.83	24.9	210	68
RA 2	11	23.5	15.17	17.97	96	58
RA 3	14	22	17.33	19.46	172	71
<i>NS</i>	26	26	34.5	42.5	521	76
NS 1	20	36	26.67	30.93	205	64
NS 2	17	17.75	19.5	18.3	172	92
NS 3	15	15.5	16.67	15.87	144	94

Obs. species stands for observed numbers of species and obs. individuals for the number of observed individuals. The completeness is the percentage of the observed species number compared to the mean of the three estimators

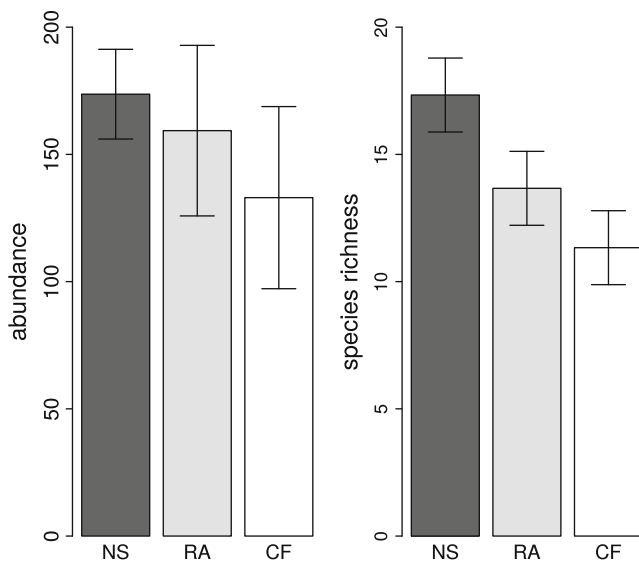


Fig. 3 Mean (\pm SE) of total abundance and species richness in the different land use types (CF corn field, RA ruderal area, NS natural savannah, n per habitat class = 3)

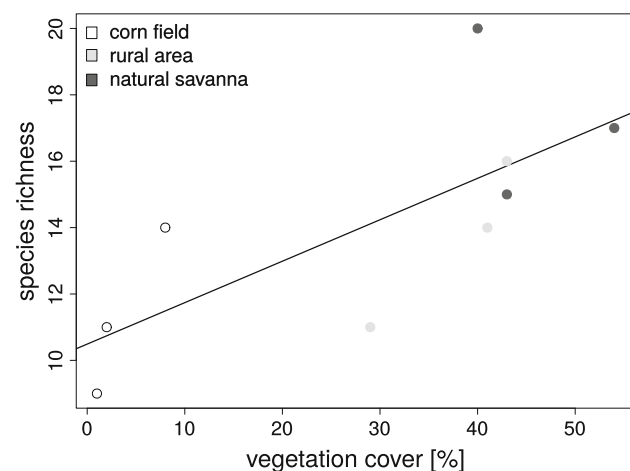


Fig. 4 Total species richness of grasshoppers per plot across a gradient of vegetation cover [%]

Community dissimilarity

The two-dimensional NMDS (Stress-value = 3.40 %) revealed a clear separation into two groups. One group contained the natural savannah plots and two ruderal area plots (RA1, RA3), and the other group the corn field plots and RA2 (Fig. 5). Vegetation cover was significantly correlated to NMDS scores and showed the best fit to the data (Table 3). Percentage of green grass showed also a good fit to the data (Table 3).

For describing the distribution of individual species in the ordination space, we focused on the most abundant species. The pattern of the species scores in the left cluster showed that

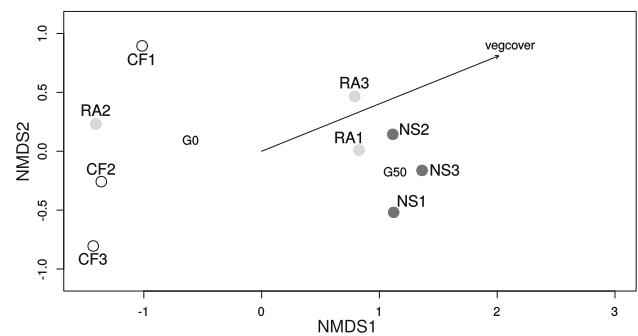


Fig. 5 Ordination graph derived from two-dimensional non-metric multidimensional scaling species abundance data. The black vector represents vegetation cover, while G0 and G50 are the centroids for categories of percentage of green grass (G0 = 0–25 %, G50 = 25–50 %). The white, gray, and dark gray circles indicate the different plots (CF = corn fields, RA = ruderal area, NS = natural savannah)

Table 3 Results of fitting three environmental variables onto the ordination

Environmental variables	r^2 value	p value
Vegetation cover	0.804	0.01
Cragginess	0.445	0.143
Percentage of green grass	0.450	0.054

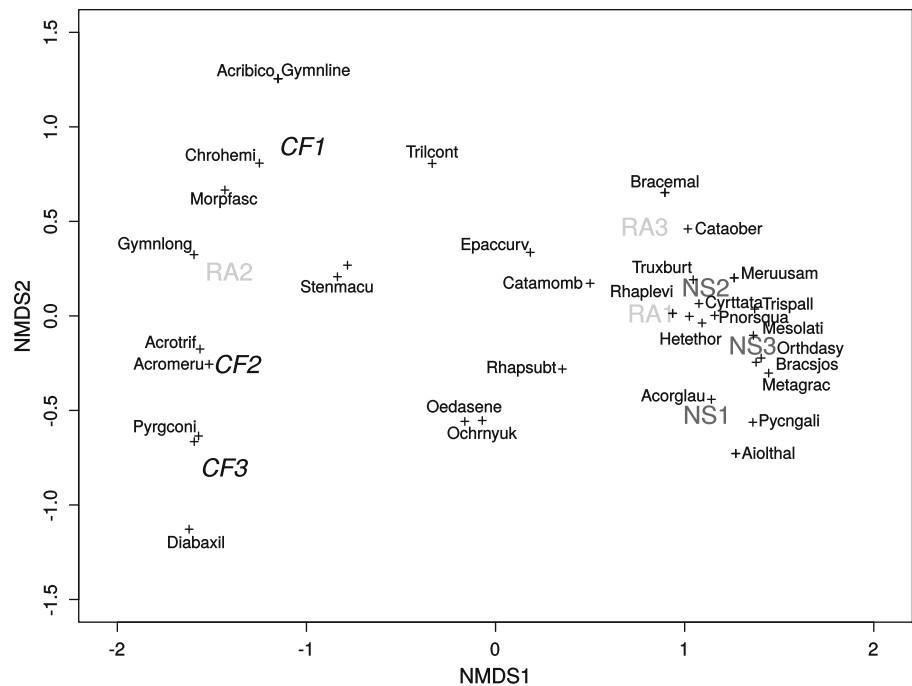
The r^2 -value is the squared correlation coefficient, which explains the goodness of fit of the parameters to the results of the NMDS. P -values are based on 999 permutations and significant values are indicated by bold font

Acrotylus meruensis and *Acrotylus trifasciatus trifasciatus* were most abundant on plots that had a high percentage of bare ground (CF2, CF3 and RA2), as well as *Chrotogonus hemipterus* which was most abundant on CF1. Also *Stenohippus maculifemur* was mostly found in ruderal areas with low vegetation cover. Six species (*Acorypha glaucopsis*, *Brachycrotaphus sjostedi*, *Pycnodictya galinieri*, *Metaxymecus gracilipes*, *Mesopsis laticornis* and *Orthochtha dasyncnemis dasyncnemis*) occurred mainly in natural savannah. While *Cataloipus oberthuri oberthuri* occurred mainly in savannah-like ruderal areas in the Lake Chala area. *Rhaphotittha levis* and *Cyrtacanthacris tatarica tatarica* were equally abundant in ruderal areas and natural savannah. While *Epacrocatantops curvicercus* and *Catantops momboensis momboensis* were the only two species that found equally in all land use types (Fig. 6, Online Resource Table 3).

Discussion

In this study we examined the effects of land conversion by small-scale subsistence farmers on short-horned grasshoppers (Orthoptera: Caelifera: Acridomorpha). The first

Fig. 6 Ordination graph derived from two-dimensional non-metric multidimensional scaling species abundance data. The black, gray, and dark gray labels indicate the different plots (CF corn fields, RA ruderal area, NS natural savannah). Each black cross constitutes one species (weighted averages scores of species). Species names are abbreviations (Online Resource Table 3). Not all species names are shown



question we addressed was: How do local grasshopper assemblages, in particular their species richness and dissimilarity, respond to land conversion. Our results showed that the models including vegetation or percentage of green grass were better supported in explaining the differences in species richness and abundance than the model including land use type. Further, for the dissimilarities in grasshopper assemblages vegetation cover appeared to be a best predictor. No rare or threatened species were found during our sampling. However, several species appeared only in one land use type. Our study suggests that the impact of land conversion on the grasshopper biodiversity is mediated by changes in the plant biomass and vegetation structure retained in agricultural systems (i.e. the habitat configuration and management) offering possibilities for sustainable land management.

Differences in total species richness and observed survey species richness were most pronounced between savannah and corn fields, while ruderal areas hosted similar numbers of species like natural savannahs. Similarly high species richness was found at sites with high vegetation cover. This is in congruence with the energy-abundance hypothesis, which states that higher net primary production, indicated by a higher vegetation cover, leads to an increased diversity (Kaspari et al. 2004). These patterns of species richness were also found in tropical and temperate grasslands due to disturbance by grazing (Samways and Kreuzinger 2001; Gebeyehu and Samways 2002; Kruess and Tscharrntke 2002; Marini et al. 2008; Branson and Sword 2010). Additionally, vegetation heterogeneity was

identified as an important factor which positively influenced species richness and grasslands with a high structural heterogeneity had higher species richness than grasslands with a homogenous structure (Craig et al. 1999; Gebeyehu and Samways 2003). We assume that this effect in concert with a higher net primary production caused the high species richness found in the ruderal areas and natural savannahs.

The different land use types showed dissimilarities in their grasshopper assemblages, but note that the environmental parameters were again a better predictor as found by other studies in Sub-saharan Africa (Samways and Kreuzinger 2001, Gebeyehu and Samways 2002). While in the natural savannah mostly species which are associated with high vegetation cover, like *Orthochtha dasyncnemis dasyncnemis* (Eterovick and Figueira 1997), were found, communities in ruderal areas were composed of species which are associated with bare ground, like those of the genus *Acrotylus* (Chappell and Whitman 1990), as well as of species associated with a high vegetation cover. In corn fields, besides some habitat generalists, no savannah species were found and several species were only collected in one land use type, suggesting species-specific responses to land conversion (e.g. Joern 1982, Chambers and Samways 1998).

A mosaic of transformed and natural/semi-natural habitats can still maintain a high diversity (Vrdoljak and Samways 2014). In congruence our results indicate the opportunity that a small-scale agricultural mosaic with extensively managed ruderal areas may maintain a relative

high species richness and diversity. This is also supported by the finding that all land use types combined (unsurprisingly) had a lower sampling completeness and higher species richness than the single land use types, indicating that all three land use types had different special assemblages. Note that all our agricultural plots were in dispersal distance of natural savannah areas. In agricultural landscapes without connection to natural savannahs, which potentially serve as source habitats for grasshopper populations (Devictor and Jiguet 2007), the effects may be much more severe (Rüdisser et al. 2012). Also the configuration within the agricultural mosaic, especially the connectivity of suitable habitat, is an important deterrent for grasshopper diversity and species performance in these landscapes (Collinge and Forman 1998; Badenhausser et al. 2012; Keller et al. 2013). However, extensive agricultural management might positively influence common species, but not rare species (Steck et al. 2007), which should be an important aspect of conservation issues.

During the study in none of the land use types we collected species that are considered rare or threatened (Hemp 2009) besides *Ischnansis curvicerca* (Hemp 2013) which was once found in savannah-like ruderal areas. However, in 2013 *Alлага ambigua* was collected in natural savannah, a species listed in the IUCN red list of threatened species as critically endangered (Gereau et al. in press). Most singletons (species only found once) surprisingly occurred in the ruderal areas, followed by corn fields and then natural savannah. Though, two of the singletons occurring in cornfields and three occurring in ruderal areas were also collected in the natural savannah in opportunistic samplings during the study time, while no singletons of the natural savannah were found in the other land use types. Also, we caught a few specimens of *Stenocroblytus cervinus*, an East African endemic, known only from a few specimens, but probably with a wider distribution throughout southern Kenya, northern and central Tanzania in suitable habitats (Hemp 2013). In general, the savannah grasslands at the eastern slopes of Mt. Kilimanjaro harbour 54 different grasshopper species (Caelifera) (Hemp 2002, unpublished) and one endemic species (*Lophothericles kongoni*) as well as different rare species (e.g. *Pyrgomorphella albini*, *Usambilla turgidicrus*, *Afroxyrrhepes brevifurca*, *Abisares depressus*, *Lophothericles carinifrons*) (Hemp 2009). Also, these areas are important breeding habitats for several species of which the adults move to higher elevations (Hemp 2009). Since we did not include nymphs in our sampling, the effects of land conversion for these species might be more severe.

The effects of land conversion from natural savannah to small-scale subsistence farms on species richness and community dissimilarity are linked to environmental parameters, especially to vegetation cover. This suggests that an agricultural mosaic landscape in tropical savannah regions consisting of small-scale farms, extensive managed

ruderal areas and remnants of natural savannah may maintain high species richness. Therefore, the value of these mosaics for grasshopper and insect conservation will strongly depend on the habitat configuration and farm management, especially the amount of plant biomass retained on fields and might be diminished in the future with continuing agricultural intensification. Past years have seen a dramatic decrease of natural savannah habitats and intensification of corn production in East Africa. As most savannah species will not find a suitable habitat in corn fields, an increasing expansion of agriculture and the correlated fragmentation of natural savannah habitats may successively endanger many species which are currently still common and widely distributed.

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References

- Altieri MA (1999) The ecological role of biodiversity in agroecosystems. *Agric Ecosyst Environ* 74:19–31
- Andersen AN, Ludwig JA, Lowe LM, Rentz DCF (2001) Grasshopper biodiversity and bioindicators in Australian tropical savannas: responses to disturbance in Kakadu National Park. *Austral Ecol* 26:213–222
- Appelhans T, Mwangomo E, Otte I, Detsch F, Nauss T, Hemp A (2014) Monthly and annual climate data averaged from 2011 to 2013 for 79 research plots on the southern slopes of Mt. Kilimanjaro. V 1.0. ZENODO. doi: [10.5281/zenodo.11695](https://doi.org/10.5281/zenodo.11695)
- Badenhausser I, Gouat M, Goarant A, Crnulic T, Bretagnolle V (2012) Spatial autocorrelation in farmland grasshopper assemblages (Orthoptera: Acrididae) in Western France. *Environ Entomol* 41:1050–1061
- Barton K (2012) MuMIn: Model selection and model averaging based on information criteria. R package version 1.12-1. <http://CRAN.R-project.org/package=MuMIn>. Accessed 20 Jan 2015
- Batáry P, Orci KM, Báldi A, Kleijn D, Kisbenedek T, Erdős S (2007) Effects of local and landscape scale and cattle grazing intensity on Orthoptera assemblages of the Hungarian Great Plain. *Basic Appl Ecol* 8:280–290
- Belovsky GE (2000) Do grasshoppers diminish productivity? a new perspective for control based on conservation. In: Lockwood J, Latchinsky A (eds) *Grasshoppers, locusts and grassland health*. Kluwer Academic Publishers, Dordrecht, pp 7–29
- Bjornstad ON (2013) ncf: Spatial nonparametric covariance functions. R package version 1.1-5. <http://CRAN.R-project.org/package=ncf> Accessed 23 Jan 2015
- Bock CE, Bock JH (1991) Response of grasshoppers (Orthoptera: Acrididae) to wildfire in a southeastern Arizona grassland. *Am Midl Nat* 125:162–167

- Borcard D, Gillet F, Legendre R (2011) Numerical ecology with R. Springer, New York
- Branson DH, Sword GA (2010) An experimental analysis of grasshopper community responses to fire and livestock grazing in a northern mixed-grass prairie. *Environ Entomol* 39:1441–1446
- Branson DH, Joern A, Sword GA (2006) Sustainable management of insect herbivores in grassland ecosystems: new perspectives in grasshopper control. *Bioscience* 56:743–755
- Chambers BQ, Samways MJ (1998) Grasshopper response to a 40-year experimental burning and mowing regime, with recommendations for invertebrate conservation management. *Biodivers Conserv* 7:985–1012
- Chappell MA, Whitman DW (1990) Grasshopper thermoregulation. In: Chapman RF, Joern A (eds) *Biology of grasshoppers*. Wiley, New York, pp 143–172
- Collinge SK, Forman RTT (1998) A conceptual model of land conversion processes: predictions and evidence from a microlandscape experiment with grassland insects. *Oikos* 82:66–84
- Craig DP, Bock CE, Bennett BC, Bock JH (1999) Habitat relationships among grasshoppers (Orthoptera: Acrididae) at the western limit of the Great Plains in Colorado. *Am Midl Nat* 142:314–327
- Devictor V, Jiguet F (2007) Community richness and stability in agricultural landscape: the importance of surrounding habitat. *Agric Ecosyst Environ* 120:179–184
- Eterovick PC, Figueira JEC (1997) Cryptic coloration and choice of escape microhabitats by grasshoppers (Orthoptera: Acrididae). *Biol J Linn Soc* 61:485–499
- Faith DP, Minchin PR, Belbin L (1987) Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69:57–68
- Gandar MV (1980) Short term effects of the exclusion of large mammals and insects in broad leaf savannah. *S Afr J Sci* 76:29–31
- Gandar MV (1982) The dynamics and trophic ecology of grasshoppers (Acridoidea) in a South African savannah. *Oecologia* 54:370–378
- Gebehehu S, Samways MJ (2002) Grasshopper assemblage response to a restored national park (Mountain Zebra National Park, South Africa). *Biodivers Conserv* 11:283–304
- Gebehehu S, Samways MJ (2003) Responses of grasshopper assemblages to long-term grazing management in a semi-arid African savannah. *Agric Ecosyst Environ* 95:613–622
- Gereau RE, Cordeiro N, Cumberlidge N, Hemp C, Hochkirch A, Jones T, Kariuki M, Lange C, Loader SP, Malonza PK, Menegon M, Ndong'ang'a PK, Rovero F, Shirk P (in press) Globally threatened biodiversity of the Eastern Arc mountains and coastal forests of Kenya and Tanzania. *J East Afr Nat Hist*
- Gillon Y (1972) The effect of bush fire on the principal acridid species of and Ivory Coast savanna. *Proc Tall Timbers Fire Ecol Conf* 11:419–471
- Gillon Y (1983) The invertebrates of the grass layer. In: Bouliere F (ed) *Ecosystems of the world 13: tropical savannahs*. Elsevier, Amsterdam, pp 289–311
- Haberl H, Erb KH, Krausmann F, Gaube V, Bondeau A, Plutzer C, Gingrich S, Lucht W, Fischer-Kowalski M (2007) Quantifying and mapping the human appropriation of net primary production in Earth's terrestrial ecosystems. *Proc Natl Acad Sci USA* 104:12942–12947
- Havemann T, Muccione V (2011) Mechanisms for agricultural climate change mitigation incentives for smallholders. CCAFS Report no. 6. CGIAR research program on climate change, agriculture and food security (CCAFS). Copenhagen, Denmark
- Hemp C (2002) New Acrometopae from East Africa (Tettigoniidae: Phaneropterinae). *J Orthoptera Res* 11:67–76
- Hemp A (2006) Vegetation of Kilimanjaro: hidden endemics and missing bamboo. *Afr J Ecol* 44:305–328
- Hemp C (2009) Annotated list of Caelifera (Orthoptera) of Mt. Kilimanjaro, Tanzan. *J Orthoptera Res* 18:183–214
- Hemp C (2013) Annotated list of Ensifera (Orthoptera) and further records on Caelifera (Orthoptera) of Mt. Kilimanjaro. *Tanzan Zootaxa* 3613:301–342
- Hochkirch A, Adorf F (2007) Effects of prescribed burning and wildfires on Orthoptera in Central European peat bogs. *Environ Conserv* 34:225–235
- Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. *Biom J* 50:346–363
- Joern A (1982) Vegetation structure and microhabitat selection in grasshoppers (Orthoptera, Acrididae). *Southwest Nat* 27:197–209
- Joern A, Gaines SB (1990) Population dynamics and regulation in grasshoppers. In: Chapman RF, Joern A (eds) *Biology of grasshoppers*. Wiley, New York, pp 415–482
- Joern A, Laws AN (2013) Ecological mechanisms underlying arthropod species diversity in grasslands. *Annu Rev Entomol* 58:19–36
- Kaspari M, Ward PS, Yuan M (2004) Energy gradients and the geographic distribution of local ant diversity. *Oecologia* 140:407–413
- Keller D, van Strien MJ, Herrmann M, Bolliger J, Edwards PJ, Ghazoul J, Holderegger R (2013) Is functional connectivity in common grasshopper species affected by fragmentation in an agricultural landscape? *Agric Ecosyst Environ* 175:39–46
- Kemp WP (1992) Rangeland grasshopper (Orthoptera: Acrididae) community structure: a working hypothesis. *Environ Entomol* 21:461–470
- Kruess A, Tscharnkte T (2002) Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. *Conserv Biol* 16:1570–1580
- Lockwood JA (1997) Rangeland grasshoppers ecology. In: Gangwere SK, Muralirangan MC, Muralirangan M (eds) *The bionomics of grasshoppers, katydids and their kin*. CABInternational, Wallingford, pp 83–101
- Marini L, Fontana P, Scotton M, Klimek S (2008) Vascular plant and Orthoptera diversity in relation to grassland management and landscape composition in the European Alps. *J Appl Ecol* 45:361–370
- Mbonile MJ, Misana BM, Sokoni C (2003) Land use change patterns and root causes on the southern slopes on Mount Kilimanjaro, Tanzania. Land use change impacts and dynamics (LUCID) Project Working Paper 25. International Livestock Research Institute, Nairobi
- Millennium Ecosystem Assessment (2005) *Ecosystems and human well-being: synthesis*. World Resources Institute, Washington, DC
- Miller RH, Onsager JA (1991) Grasshopper (Orthoptera: Acrididae) and plant relationships under different grazing intensities. *Environ Entomol* 20:807–814
- Minchin PR (1987) An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* 69:89–107
- Nagayets O (2005) Small farms: current status and key trends. The future of small farms: Proceedings of a research workshop, Wye, UK
- O'Neill KM, Olson BE, Rolston MG, Wallander R, Larson DP, Seibert CE (2003) Effects of livestock grazing on rangeland Orthoptera (Orthoptera: Acrididae) abundance. *Agric Ecosyst Environ* 97:51–64
- Oksanen J, Guillaume Blanchet F, Kindt R, Legendre P, O'Hara RB, Simpson GL, Solymos R, Stevens MHH, Wagner H (2011) *vegan: community ecology package*. R package version 1.17-7. <http://CRAN.R-project.org/package=vegan> Accessed 24 March 2011
- Pinheiro J, Bates D, DebRoy S, Sarkar D, the R Development Core Team (2011) *nlme: Linear and Nonlinear Mixed Effects Models*.

- R package version 3.1-98. <http://CRAN.R-project.org/package=nlme>. Accessed 02 March 2011
- Quinn MA, Johnson PS, Butterfield CH, Walgenbach DD (1993) Effect of grasshopper (Orthoptera: Acrididae) density and plant composition on growth and destruction of grasses. *Environ Entomol* 22:993–1002
- R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical computing, Vienna, Austria. <http://www.r-project.org>
- Rüdiger J, Tasser E, Tappeiner U (2012) Distance to nature—a new biodiversity relevant environmental indicator set at landscape level. *Ecol Indic* 15:208–216
- Samways MJ (1994) *Insect conservation biology*. Springer, New York
- Samways MJ (1997) Conservation biology of Orthoptera. In: Gangwere SK, Muralirangan MC, Muralirangan M (eds) *The bionomics of grasshoppers, katydids and their kin*. CAB International, Wallingford, pp 481–496
- Samways MJ, Kreuzinger K (2001) Vegetation, ungulate and grasshopper interactions inside vs. outside an Africa savannah game park. *Biodiv Conserv* 10:1963–1981
- Samways MJ, Sergeev MG (1997) Orthoptera and Landscape Change. In: Gangwere SK, Muralirangan MC, Muralirangan M (eds) *The bionomics of grasshoppers, katydids and their kin*. CAB International, Wallingford, pp 147–159
- Steck CE, Bürgi M, Bolliger J, Kienast F, Lehmann A, Gonthier Y (2007) Conservation of grasshopper diversity in a changing environment. *Biol Conserv* 138:360–370
- Strimmer K (2008) Fdrtool: a versatile R package for estimating local and tail area-based false discovery rates. *Bioinformatics* 24:1461–1462
- UNDP, Unep, World Bank and WRI (2000) *A guide to world resources 2000–2001: people and ecosystems: a fraying web of life*. World Resources Institute, Washington, DC
- Vrdoljak SM, Samways MJ (2014) Agricultural mosaics maintain significant flower and visiting insect biodiversity in a global hotspot. *Biodiv Conserv* 23:133–148
- Walther BA, Moore JL (2005) The concepts of bias, precision and accuracy, and their use in testing the performance of species richness estimators, with a literature review of estimator performance. *Ecography* 28:815–829
- Zhou Y (2011) *Smallholder Mapping II: trends in demographics and driving forces*. Syngenta Foundation for Sustainable Agriculture