Original Research Article

Influence of sugarcane plantations on the population dynamics and community structure of small mammals in a savanna-agricultural landscape

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ABSTRACT

Conversion of native habitats into agricultural monocultures is a major cause of biodiversity loss favouring a small number of generalist species. Rodents can cause significant declines in crop yield, hence understanding the factors affecting their population dynamics is of importance to the agricultural sector. Sugarcane plantations in African savannas harbour a low diversity of small mammals, with a single genus (*Mastomys* spp.) often dominating the community. Our study investigated the factors that shape the composition of the small mammal community and the life-history traits of the dominant species in a savanna-sugarcane landscape mosaic. We surveyed small mammals at eight sites, six in sugarcane and two in neighbouring savannas at five-week intervals over the course of a year. Sugarcane and native savanna sites were categorised into vegetation height classes. We captured a total of 845 individual small mammals belonging to eight species across all sites. Species diversity was higher in the savanna than in sugarcane fields. Although the composition of the community overlapped in the two habitats, it was most similar between tall sugarcane and savanna, than between sites that had recently planted (emerging or short) sugarcane and either tall sugarcane or savanna. Furthermore, population densities of the dominant species (*Mastomys natalensis*) were significantly higher in sugarcane than in native savanna. Additionally, the interactions between habitat and season influenced survival and body condition of *M. natalensis*; apparent survival decreased in savanna and body condition improved in sugarcane during the wet season. Furthermore, the survival of *M. natalensis* was also significantly reduced in sugarcane fields that had been burnt prior to harvesting. However, there was no significant difference in the extent of breeding between the two habitats. This study provides novel insight into the mechanisms that allow for the persistence of high densities of rodent pest species.

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1. Introduction

Currently, anthropogenic activities are major causes of biodiversity loss worldwide (Butchart et al., 2010). Among them, the conversion of native habitats into monocultures has been shown to negatively alter wildlife communities (Ellis and Ramankutty, 2008; Park, 2015; Ramankutty and Foley, 1999). Indeed, this kind of alteration that fragments and homogenizes landscapes (McCleery et al., 2018; Reynolds et al., 2017) has led to reduced species richness and functional diversity, favouring generalist species at the expense of less flexible specialists (Byrom et al., 2015; Hurst et al., 2014; Soto-Shoender et al., 2018). Hitherto, research on the impact of monocultures on biodiversity has mostly focused on population and community parameters, while the effects on demography and life history traits remain poorly studied.

Non-volant small mammals, particularly rodents, provide diverse ecosystem services such as soil aeration, pollination, seed dispersal, and serve as prey for higher trophic levels (Lacher et al., 2016). Additionally, rodents are economically important as crop pests, causing damage to a large variety of crops (Singleton et al., 2010, 2005). In Africa alone, at least 25 species of rodents are known for their negative impacts on agriculture, or public health (Makundi et al., 1999). Therefore, a better understanding of the factors that shape the community structure and intraspecific demography and life history traits of non-volant small mammals is required for the effective management of their negative impacts.

Intensive sugarcane production (*Saccharum* sp.), is expanding in eastern southern Africa (Hulley, 2007). Sugarcane plantations drastically alter ecosystem conditions. Indeed, within this type of crop, vegetation composition and structure are less complex than in natural landscapes (Reynolds et al., 2017). Especially, vegetation height exhibits high temporal heterogeneity. Consequently, with plant growth, vegetation cover varies from near zero at the time of planting to very thick and matted just before harvesting (Gheler-Costa et al., 2013). This generates rapidly changing levels of cover which is an important habitat parameter for small mammals (Banasiak and Shrader, 2016; Loggins et al., 2019; Monadjem, 1997), presumably mediated through predation (Vibe-Petersen et al., 2006). Furthermore, food abundance for rodents in sugarcane plantations is probably greatly increased by irrigation. Rodent species, that have high reproductive rates and fast generation time, may be capable of taking advantage of such temporally dynamic habitats (Singleton et al., 2010).

The multimammate mouse (*Mastomys natalensis*) is a rodent that is typically associated with agricultural landscapes in sub-Saharan Africa where it is often the dominant species (Hurst et al., 2013; Makundi et al., 2007, 1999; Mohammed et al., 2017), and may become a major pest (Fiedler, 1988; Leirs et al., 1996a). Large litter size, increased survival and fast generation time, are some of the demographic parameters that favour the high population turnover of *M. natalensis* (Monadjem, 1998; Telford, 1989). These factors together with its omnivorous diet allow *M. natalensis* populations to irrupt in regions experiencing seasonal rainfall (Leirs et al., 1996a).

In the context of the significant land use changes occurring in Africa (Smith et al., 2016), it becomes important to investigate the impact of agriculture on small mammal communities. However, agricultural fields also offer ecologists a platform to conduct large-scale experiments that would not be feasible or ethical in native habitats. For example, sugarcane fields in Eswatini are carefully managed on an 11-month cycle (see Methods below), with sugarcane fields at various growth stages throughout the year, creating a mosaic of plant growth stages across seasons. This situation is made possible by irrigation and fertilization of the fields, which effectively decouples vegetation biomass and season, whereas in neighbouring native habitats, vegetation biomass is determined by rainfall which is highly seasonal (Deshmukh, 1984). Therefore, our first objective was to compare species richness and composition of the small mammal community in sugarcane with that occurring in native savanna habitat. Our second objective was to determine the influence of vegetation structure, including the different growth stages of sugarcane and burning, on life history traits of the dominant species, *M. natalensis*, in Eswatini (Hurst et al., 2014, 2013).

We expected the small mammal community to be less diverse in sugarcane plantations than in native savanna habitat. Indeed, the homogeneity and similarity in vegetation structure of sugarcane may exclude specialist species, as shown by Hurst et al. (2014). Furthermore, we expected fields with tall sugarcane to provide cover and protection from predators of *M. natalensis* (Loggins et al., 2019). Therefore, we predicted an increase in survival of this species with vegetation height. We also expected that animals in sugarcane plantations would have better body condition compared with those in native savanna, and that there would be less variation between seasons in sugarcane since fields are irrigated throughout the year. Furthermore, with animals in better condition, we predicted that animals in sugarcane would have an extended breeding season compared with those in savanna. Hence, in conclusion we expected that elevated food supply should result in an increased population density of *M. natalensis* in sugarcane fields compared with native savanna.

2. Methods and materials

2.1. Study area

The study was conducted on the estates of the Royal Swaziland Sugar Corporation and Tambankulu which are located in north-eastern Eswatini. The warmest and coolest months are January and July with daily mean temperatures of 26.1 °C and 14.6 °C, respectively. This area receives a mean annual rainfall of 574 mm. The native vegetation in this region is low-lying savanna dominated by species of *Senegalia, Vachellia* and *Dichrostachys* (Monadjem and Reside, 2008). The topography of the area is relatively flat and altitude is 150−250 m. The estates are covered by vast plantations of irrigated sugarcane together with roads, water storage, and canal systems (Kingston, 2003). There are also fragmented patches of native vegetation

scattered throughout the fields as well as patches associated with riparian areas. The growing period of the sugarcane lasts about nine months, starting from bare ground (just planted) to plants over 3 m in height. This is then followed by a period of 1–2 months of drying off when irrigation is stopped, making the total growing period about 10–11 months from planting to harvest (Rostron, 1975). To assist with harvesting, which is conducted manually in Eswatini, the sugarcane field is burnt one or a few days prior to harvesting. This is facilitated by the use of gasoline which is poured around the edge of the field; hence, the blaze begins on the outer margins and works its way to the center. Environmental conditions coupled with irrigation render the growth of sugarcane possible during the entire year meaning that harvesting of mature cane, and successive plant growth stages, are independent of the year calendar.

2.2. Study design

We randomly located six sampling grids in Simunye and Tambankulu sugarcane fields and two control grids in adjacent native savanna habitat within the Mbuluzi Game Reserve. Our sampling sites were situated between 26.095° and 26.194°S, and 31.928° and 32.002 °W. We placed all grids at least 1 km apart. Each grid had 49 (7×7) trapping stations with a single Sherman trap ($7.6 \times 9.5 \times 30.5$ cm, H.B. Sherman Live Traps. Inc, Tallahassee, Florida), with 15 m spacing between traps. We placed grids >100 m away from the borders of sugarcane fields and >100 m from patches of native vegetation found within the fields. Similarly, grids placed in native vegetation were >100 m from sugarcane fields. We classified vegetation height within the grids into four different classes: emerging ($\leq$30 cm); short (30–100 cm); medium (100–200 cm); and tall ($\geq$200 cm) (Fig. 1). To assess the height of the sugarcane (in sugarcane fields) and grass (in savanna) we measured the height of the vegetation with a long metal pole at nine locations on each grid, and used the average as the height of the vegetation.
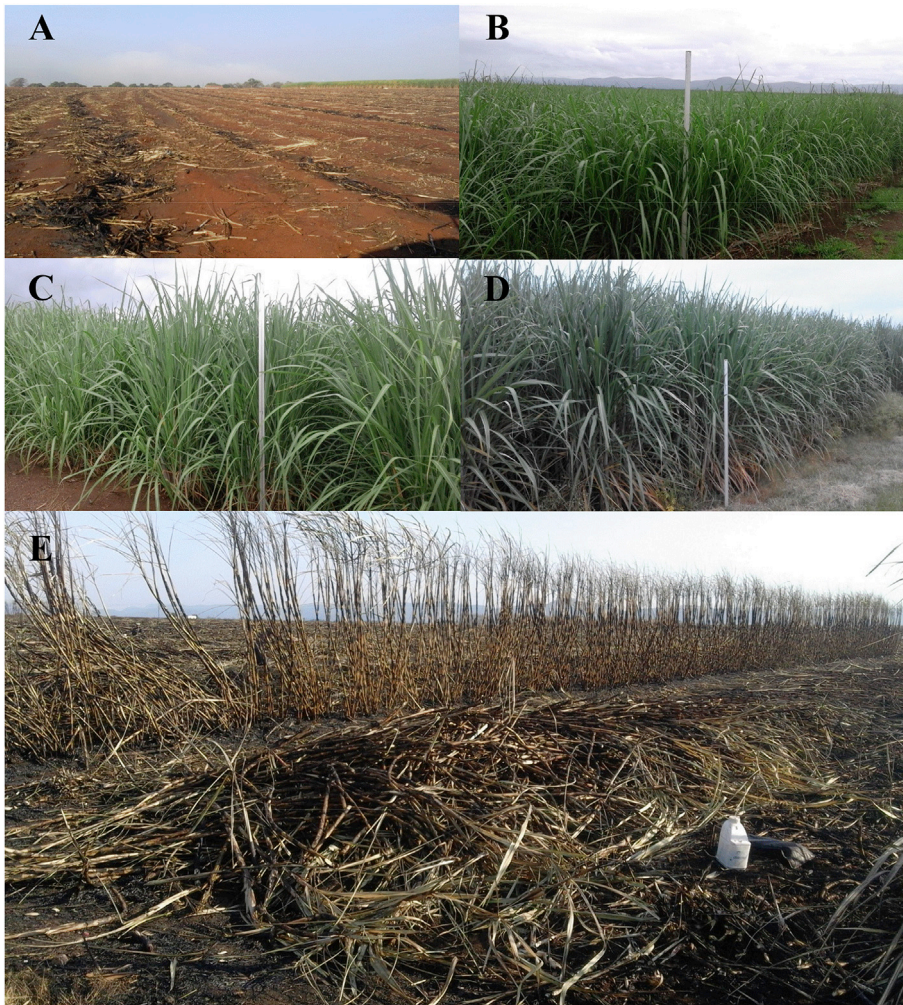

Fig. 1. The four different sugarcane height categories that were used in this study: (A) emerging sugarcane; (B) short sugarcane; (C) medium sugarcane; (D) tall sugarcane; and (E) burnt field. The metal pole is 2 m in length.

We conducted a total of ten monthly trapping sessions between June 2017 and May 2018 at five week intervals, with traps remaining active for four consecutive nights in each sampling grid. We placed Sherman traps, baited with a mixture of oatmeal and peanut butter, in full shade to prevent trapped animals from overheating. Additionally, we fitted the traps with nesting material (cotton wool) during the cold (i.e. dry) season to prevent captured animals from dying of exposure.

2.3. Data collection

Upon capture we identified, marked with an ear tag, weighed, and measured length of hindfoot of each rodent. We determined breeding condition of males by the position of the testes (scrotal vs abdominal), following Makundi et al. (2007). For females, we assessed pregnancy by palpation, and evidence of mating was associated with the occurrence of a perforated vagina (Makundi et al., 2007). We released captured animals at the point of capture.

Appropriate permits were obtained for capturing small mammals at all the sites mentioned in this study. Animal handling was conducted in accordance with the guidelines from the American Society of Mammalogists (Sikes, 2016).

2.4. Data analysis

We conducted all analyses with R version 3.5.1 (R Core Development Team, 2016). Based on our predictions, we conducted the following analyses (see below).

2.4.1. Analyses of communities

We defined species richness as the number of species present per grid and per session, while species diversity was calculated using the Shannon diversity index ($H' = \Sigma p_i \times \ln (p_i)$, where '$p_i$' represents the proportion of individuals from species 'i' (Krebs, 2014). Species richness and species diversity were calculated using habitats (sugarcane plantation vs savanna), vegetation height (four classes), season (dry vs wet), and the interaction between habitat and season as explanatory variables. We ran a linear mixed model for species diversity (function: "lmer", package: "lmerTest" (Kuznetsova et al., 2017)) and a generalized linear mixed model fitted for Poisson distributions (function: "glmer", package: "lme4" (Bates et al., 2015)) for species richness. In both cases the grid ID was included as a random factor. The interaction terms were removed if not significant (Engqvist, 2005). For the treatment effect, pairwise Tukey post-hoc comparisons were conducted using the function: "glht", in the package "multcomp" (Hothorn et al., 2008).

Additionally, we investigated species composition of the small mammal community using Non-Metric Multi-Dimensional Scaling (NMDS), conducted using Bray-Curtis similarities. Analysis of Similarities (one-way ANOSIM) was used to determine differences between the treatments and control. Both these analyses were conducted in Primer 5.2 (http://www.primer-e.com).

2.4.2. Population density

We used the minimum number alive method (Krebs, 1999) to estimate the relative densities of the three most abundant species of rodents in our study (i.e. *Mastomys natalensis, Lemniscomys rosalia* and *Mus minutoides*) on each grid. We then analysed these densities per grid and per session using generalized linear mixed models fitted for Poisson distributions (function: "glmer", package: "lme4" (Bates et al., 2015)). As explanatory variables, we included habitat (sugarcane vs. savanna), vegetation height (the four classes mentioned above), season (dry vs wet) and the interaction between season and habitat. We used the grid ID as a random factor. The interaction terms were removed if not significant (Engqvist, 2005). Pairwise Tukey post-hoc comparisons for the treatment effect were conducted using the function "glht" in the package "multcomp" (Hothorn et al., 2008).

2.4.3. Survival analysis

We estimated apparent survival probability from one session to another using a Cormack-Jolly-Seber model with a Bayesian interference (Kery and Schaub, 2012) calling the function "jags" from the R-package "jagsUI" (Kellner, 2018). We scored the apparent state of each individual as dead or alive for each session. On first capture both the apparent state and the capture probability of an individual was 1. We modelled subsequent states through Bernoulli trials. The success probability corresponded to the product of the apparent state of the individual during the previous session and the apparent survival probability. We modelled variation in apparent survival as a function of habitat (sugarcane vs savanna), vegetation height (the four height categories mentioned above plus a fifth category of burnt field), season (dry vs wet), sex (female vs male) and the interaction between season and habitat. Moreover, we considered the grid ID and the sessions as random effects of the survival probability. The constructed function was logit-transformed. The capture history matrix comprised the capture state (captured or not captured) of each individual during each session. The capture states corresponded to realizations of Bernoulli trials, with the product of the related apparent states and the capture probability as success parameters.

We specified vague prior distributions for the modelled coefficients (i.e. normal distributions with mean of 0 and precision of 0.001, constrained between -10 and 10, for the regression parameters (i.e. the intercept and covariate effects for the survival probability), uniform distributions [0,5] for the standard deviation of the random factors, which had a mean of 0) and uniform distribution [0,1] for the capture probability. We ran three different Markov chains, starting at random initial values in the range of parameter space, for 50,000 iterations with a 20,000 iteration burn in. Markov chains were thinned by a factor

of 3 and the Brooks-Gelman-Rubin criterion R̂ was used to assess the convergence of chains, indicated when R̂ < 1.1 (Brooks and Gelman, 1998). Effects, with a posterior distribution 95% credible interval (95% CRI) not covering 0, were considered as significant.

2.4.4. Body condition

We assessed variation in body condition using the body mass as response variable and a size variable (i.e. hindfoot length) as covariate (García-Berthou, 2001). We used a linear mixed model, (function: "lmer", package: "lmerTest" (Kuznetsova et al., 2017)) where explanatory variables comprised hindfoot length, season (dry vs wet), habitat (sugarcane vs savanna), sex (female vs male) and the interaction between season and habitat. The interaction term was removed if not significant. The grid ID was considered as a random factor.

2.4.5. Breeding

We analysed the breeding status of *M. natalensis* per session and per grid using a generalized mixed model (function: "glmer", package: "lme4" (Bates et al., 2015)). Season (dry vs wet), habitat (sugarcane vs savanna), sex, and the interaction between season and habitat were considered as fixed effects. We used grid ID as a random factor and removed the interaction term if it was not significant.

3. Results

3.1. Influence of growth stages on community structure

We captured a total of 845 individual small mammals during 15,680 trap nights in 10 sampling sessions (capturing success = 5.4%). We recorded a total of eight small mammal species, comprising seven rodents (Rodentia) and one shrew (Soricomorpha) species. Rodents included *Mastomys natalensis* (Natal multimammate mouse), *Lemniscomys rosalia* (Single-striped grass mouse), *Mus minutoides* (Pygmy mouse), *Aethomys ineptus* (Tete veld rat), *Rattus rattus* (Black rat), *Dendromus mystacalis* (Chestnut climbing mouse) and *Saccostomus campestris* (Pouched mouse). Shrews were represented by *Crocidura hirta* (Lesser red musk shrew). *Mastomys natalensis* was the most commonly trapped species representing 56.7% of all captures followed by *L. rosalia* (Table 1); these two species accounted for 86.2% of all captures. The numbers of *A. ineptus*, *S. campestris*, *D. mystacalis* and *R. rattus* were comparatively lower. Furthermore, *A. ineptus* was exclusively recorded in savanna habitat while *D. mystacalis* and *R. rattus* were each captured only once (Table 1).

The interactions between habitat and season were not significant in explaining species richness (z = 0.586, p = 0.558) nor species diversity (t = 1.278, p = 0.205), and were therefore removed from the final models. Furthermore, none of the fixed effects significantly explained the variation in species richness (Table 2). Species diversity was significantly higher in savanna than in sugarcane plantations, but did not vary between seasons (Table 2, Fig. 2). Pairwise comparisons of grids with different vegetation height classes revealed that species diversity was almost always higher in a grid with taller grass, regardless of whether it was in savanna or sugarcane. Except between sites that had emerging and short vegetation, and medium and tall vegetation, all other differences were significant (Table 2).

Additionally, there was significant overlap in species composition of small mammals between the various grids in sugarcane fields and those in savanna (ANOSIM, R = 0.18, p < 0.05), however, the composition in native habitats was most similar to that of fields with medium and tall sugarcane and practically no overlap with emerging or short fields (Fig. 3).

3.2. Population density

Mastomys natalensis densities were 2.64 times higher in sugarcane than in savanna, while *L. rosalia* showed the reverse pattern, (i.e. 2.19 times higher density in the savanna). Densities of *M. minutoides* did not significantly differ between the two habitats (Tables 1 and 3). Densities of *M. natalensis* were 1.25 times lower during the wet compared to the dry season (Tables 1

Table 1
Small mammal species trapped in different sugarcane height classes and in native savanna during the wet and dry season.

Species	Emerging		Short		Medium		Tall		Savanna		TOTAL
	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	
Mastomys natalensis	32	14	68	26	11	47	120	154	28	50	**550**
Lemniscomys rosalia	3	0	16	5	11	26	53	88	46	38	**286**
Mus minutoides	1	2	7	0	3	2	10	20	12	24	**81**
Crocidura hirta	1	1	3	1	0	5	11	14	0	1	**37**
Aethomys ineptus	0	0	0	0	0	0	0	0	2	6	**8**
Dendromus mystacalis	0	0	0	0	0	0	0	0	1	0	**1**
Saccostomus campestris	0	0	0	0	0	0	1	0	1	4	**6**
Rattus rattus	0	0	0	0	0	0	1	0	0	0	**1**
TOTAL	**37**	**17**	**94**	**32**	**25**	**80**	**196**	**276**	**90**	**123**	**970**

Table 2
Results of GLMM fitted to Poisson distribution for the relationship between species richness/diversity and habitat, season, and vegetation height categories: 1 = emerging; 2 = short; 3 = medium; and 4 = tall sugarcane.

|	Estimate ± SD	z/t	p
Species richness			
Intercept	0.29 ± 0.42	0.70	0.487
Habitat	0.29 ± 0.19	1.56	0.118
Season	0.02 ± 0.14	0.14	0.888
Category 2 - 1	0.07 ± 0.27	0.26	0.994
Category 3 - 1	0.38 ± 0.26	1.47	0.451
Category 4 - 1	0.40 ± 0.26	1.54	0.410
Category 3 - 2	0.31 ± 0.21	1.46	0.460
Category 4 - 2	0.33 ± 0.22	1.51	0.425
Category 4 - 3	0.02 ± 0.20	0.09	1.000
Species diversity			
Intercept	0.10 ± 0.17	0.59	0.557
Habitat	0.26 ± 0.08	3.22	0.002
Season	0.00 ± 0.06	0.03	0.979
Category 2 - 1	0.05 ± 0.11	0.46	0.967
Category 3 - 1	0.36 ± 0.11	3.34	0.005
Category 4 - 1	0.37 ± 0.10	3.58	0.002
Category 3 - 2	0.31 ± 0.09	3.32	0.005
Category 4 - 2	0.32 ± 0.09	3.57	0.002
Category 4 - 3	0.01 ± 0.09	0.09	1.000
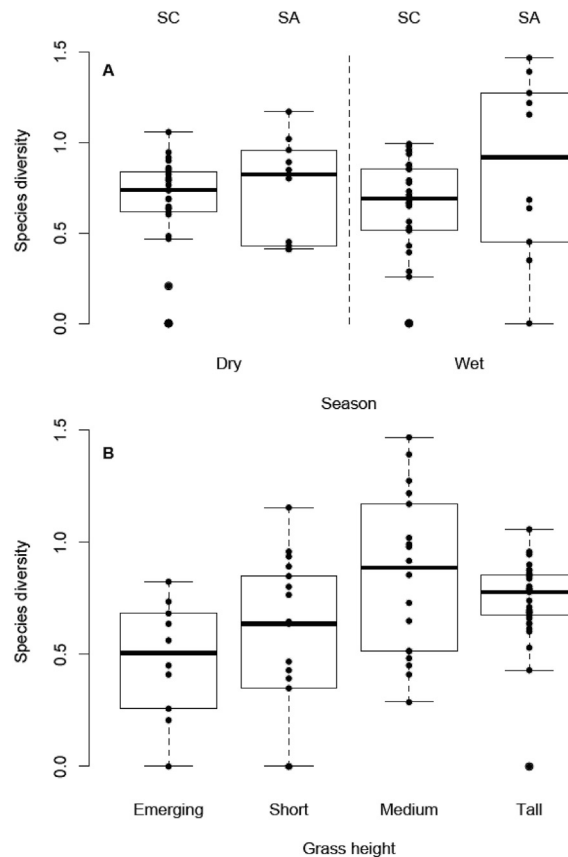
Fig. 2. Species diversity of small mammals in: (A) sugarcane (SC) and native savanna (SA) habitats in the wet and dry seasons; and (B) in fields of varying vegetation height classes.

and 3). Densities of L. rosalia did not differ significantly between seasons (Tables 1 and 3). The change in *M. minutoides* densities between the wet and dry season was 2.85 times superior in the savanna compared to the sugarcane plantations (interaction effect: Table 3). The interactions between season and habitat were not significant for *M. natalensis* (interaction effect: z = 0.55,
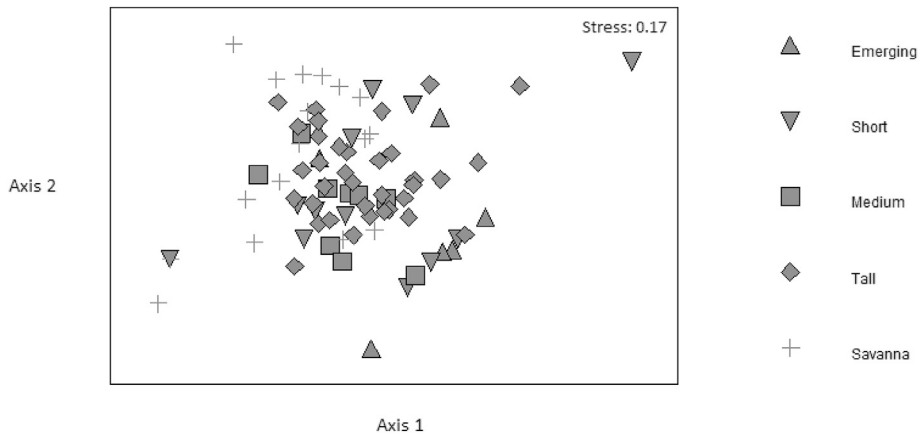
Fig. 3. Non-metric multi-dimensional scaling plot showing small mammal composition in the various growth stages of sugarcane and native savanna habitats.

Table 3
Results of GLMM fitted to Poisson distribution for the relationship between the population densities of the three most abundant rodents in sugarcane fields, *Mastomys natalensis, Lemniscomys rosalia* and *Mus minutoides*, and habitat, season, and vegetation height categories: 1 = emerging; 2 = short; 3 = medium; and 4 = tall sugarcane. Also included is the interaction between season and habitat for *M. minutoides*.

	Estimate ± SD	z	p
M.natalensis			
Intercept	3.42 ± 0.35	9.66	<0.001
Habitat	-0.97 ± 0.25	-3.95	<0.001
Season	-0.22 ± 0.07	-3.04	0.002
Category 2 - 1	0.47 ± 0.15	3.18	0.008
Category 3 - 1	0.35 ± 0.15	2.43	0.069
Category 4 - 1	0.35 ± 0.13	2.69	0.034
Category 3 - 2	-0.12 ± 0.12	-1.00	0.745
Category 4 - 2	-0.12 ± 0.10	-1.17	0.639
Category 4 - 3	-0.00 ± 0.10	-0.03	1.000
L. rosalia			
Intercept	0.00 ± 0.42	0.02	0.987
Habitat	0.78 ± 0.23	3.42	<0.001
Season	-0.13 ± 0.10	-1.37	0.172
Category 2 - 1	0.83 ± 0.24	5.29	0.003
Category 3 - 1	0.60 ± 0.24	3.44	0.051
Category 4 - 1	1.25 ± 0.24	2.54	<0.001
Category 3 - 2	-0.23 ± 0.14	5.29	0.382
Category 4 - 2	0.42 ± 0.15	-1.58	0.021
Category 4 - 3	0.65 ± 0.15	4.20	<0.001
M. minutoides			
Intercept	-2.00 ± 1.50	-1.33	0.182
Habitat	-0.12 ± 0.94	-0.12	0.901
Season	-1.35 ± 0.75	-1.80	0.072
Season:Habitat	1.05 ± 0.48	2.18	0.029
Category 2 - 1	1.87 ± 0.76	2.46	0.060
Category 3 - 1	1.61 ± 0.75	2.14	0.127
Category 4 - 1	2.11 ± 0.79	2.66	0.034
Category 3 - 2	-0.26 ± 0.31	-0.85	0.821
Category 4 - 2	0.24 ± 0.38	0.62	0.922
Category 4 - 3	0.50 ± 0.40	1.23	0.589

p = 0.584) and *L. rosalia* (interaction effect: z = 1.30, p = 0.193). Pairwise comparisons showed that *M. natalensis* densities in emerging grids were significantly lower than in short or tall sites (Tables 1 and 3). For *L. rosalia*, population densities in tall fields were significantly higher than in all other categories, and populations in short fields were at densities that were 2.28 times higher than those in emerging fields (Tables 1 and 3). Similarly, population densities of *M. minutoides* in tall fields were 8.22 times higher than those found in emerging fields (Tables 1 and 3). Other pairwise comparisons between different treatments did not reveal significant changes in *M. minutoides* population densities (Tables 1 and 3).

3.3. Apparent survival analysis

The apparent survival of *M. natalensis* did not differ significantly between habitats (Table 4). Survival was significantly reduced during the wet season in the savanna compared with that in sugarcane (interaction effect, Table 4, Fig. 4). In the sugarcane plantations, survival did not differ between seasons (Table 4). Apparent survival was significantly reduced in fields that had been burnt compared to medium or tall fields of sugarcane (Table 4).

3.4. Body condition

Body mass was significantly correlated with hindfoot length (Table 5). Body condition of individuals in the sugarcane was significantly better during the wet season than in the savanna (interaction term, Table 5). Finally, males were in better condition than females (Table 5).

3.5. Breeding

Mastomys natalensis bred significantly more during the wet season than during the dry season (2.51 ± 0.18, $z = 13.43$, $p < 0.001$). Furthermore, breeding was not significantly different in savanna compared with sugarcane (-0.72 ± 0.39, $z = -1.86$, $p = 0.063$). A higher proportion of males was observed in breeding condition than females (0.90 ± 0.18, $z = 4.92$, $p < 0.001$). The interaction between habitat and season did not significantly affect breeding status ($z = -0.85$, $p = 0.394$), and was consequently removed from the model.

4. Discussion

Our study has demonstrated substantial differences in the structure of small mammal communities between sugarcane plantations and native habitats in a savanna-agriculture landscape. Furthermore, our study has revealed a highly dynamic and rapidly changing small mammal community within the growing sugarcane fields. Species diversity was reduced in sugarcane fields, particularly at early stages of plant growth. Associated with these differences in community structure, were differences in abundance of the dominant species *Mastomys natalensis*, densities being almost 40% higher in irrigated sugarcane fields. This corroborates the findings of Hurst et al. (2013, 2014) and other researchers comparing small mammal communities in agricultural fields with neighbouring savannas in Africa (Byrom et al., 2015; Makundi et al., 2009; Monadjem, 1999a). However, because of our experimental design, we were also able to reveal differences in life history parameters of *M. natalensis* in sugarcane versus native savanna, which we suggest may explain the reported differences in its population densities reported here and in previous studies.

4.1. Community structure

Species diversity and composition varied greatly between sites depending on plant cover. Fields with tall sugarcane had similar species diversity and composition to neighbouring native savanna vegetation, but relatively bare fields (with recently planted sugarcane) were significantly different being mostly dominated by a single species *M. natalensis*. Thus, the structure of the small mammal community is highly dynamic, starting with *M. natalensis* dominating fields in the early stages of growth and progressing to a diverse community resembling that typical of savanna in later stages of sugarcane growth. In fact, this

Table 4
Results of GLMM fitted to Poisson distribution for the relationship between the survival rate of the dominant small mammal species in sugarcane, *Mastomys natalensis*, and habitat, season, and vegetation height categories: 1 = emerging; 2 = short; 3 = medium; and 4 = tall sugarcane. Also included is the interaction between season and habitat.

|	Estimate	Lower 95%CRI	Upper 95%CRI
Intercept	0.759	−0.269	1.858
Habitat	−0.355	−1.968	1.102
Season	−0.480	−1.210	0.199
Sex	−0.505	−0.923	−0.102
Season:Habitat	−1.580	−3.238	−0.044
Category 2-1	−0.286	−1.211	0.620
Category 3-1	−0.132	−1.019	0.738
Category 4-1	−0.244	−1.056	0.542
Category 5-1	−1.102	−2.221	0.020
Category 3-2	0.155	−0.577	0.880
Category 4-2	0.043	−0.543	0.616
Category 4-3	−0.112	−0.690	0.448
Category 5-2	−0.815	−1.756	0.109
Category 5-3	−0.970	−1.890	−0.067
Category 5-4	−0.858	−1.708	−0.018
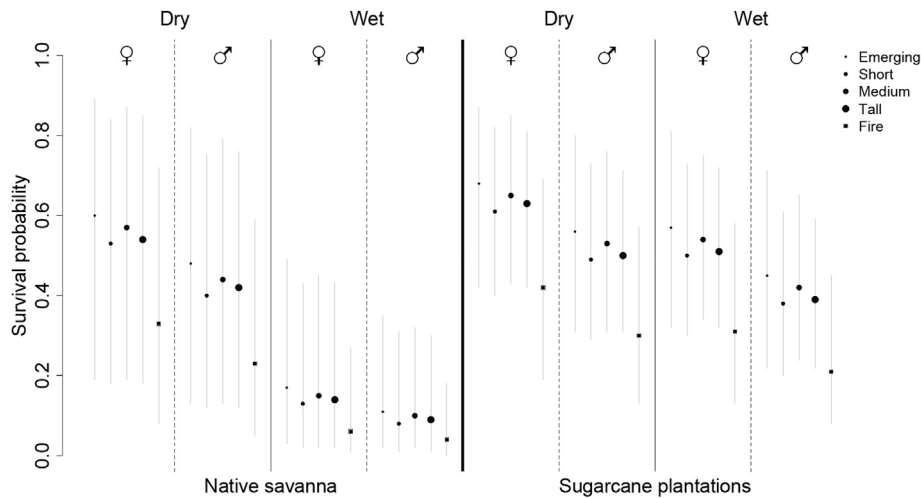
Fig. 4. Survival of *Mastomys natalensis* males and females in sugarcane and savanna during the wet and dry seasons.

closely mirrors the dynamism of small mammal communities in native grasslands following a seasonal cycle or a fire (Avenant and Cavallini, 2007; Monadjem and Perrin, 2003). However, even in the tallest sugarcane fields, species diversity does not quite reach the same levels as in native savanna. For example, granivorous species such as *Saccostomus campestris, Dendromys mystacalis* and *Aethomys ineptus* are effectively absent from sugarcane fields (Hurst et al., 2014), and this was clearly seen in our study as well (see Table 1).

4.2. Population densities, survival and breeding

Increased rodent populations in agricultural landscapes have been documented widely in Africa (Hurst et al., 2013; Leirs and Verheyen, 1995). These increased densities are usually attributed to higher food supply (Mulungu et al., 2015) with outbreaks linked to increased rainfall (Leirs et al., 1996a), yet the exact mechanisms of population proliferation are poorly understood. In this study, we show significant interactions between habitat and season in explaining lower savanna-related gain in body condition and reduction in survival during the wet season. We therefore suggest that rodents in sugarcane fields are better able to maintain body condition and survival throughout the year than in native savanna.

Good body condition is critical for breeding rodents (Field, 1975), and the ability to rapidly improve body condition after the lean dry season should allow for an earlier onset of breeding in sugarcane fields. However, we found no evidence for this in our study; males and females were reproductively active over the same time period in sugarcane fields and native savanna. It has been suggested that the plant compound 6-methoxybenzoxazolinone (6-MBOA), contained in sprouting grasses, may trigger reproduction in herbivorous rodents (Alibhai, 1986; Linn, 1991). Although we did not measure concentrations of this compound in sugarcane, it is presumably available in significant quantities within sugarcane fields throughout the year. Indeed, sugarcane plants are constantly green with sprouting young leaves (Epstein et al., 1986). The role of 6-MBOA on rodent reproduction in sugarcane fields remains to be tested, but we speculate that females in sugarcane plantations have larger litter sizes than those in native savanna, although we did not measure this.

Population growth is dependent on recruitment (reproduction) and survival. We have demonstrated that survival was better maintained across seasons in sugarcane fields than in native savanna, due to a decrease in survival during the wet season in the latter habitat. This seemingly counterintuitive result can be explained by the fact that *M. natalensis* breeds during the wet season in Eswatini (Monadjem, 1998), resulting in an increase of juvenile mice during this season, which have lower survival rates than adults (Hawlena et al., 2006). Furthermore, breeding represents drastic energy expenditure which can be translated into lower survival in adults too (Koivula et al., 2003). However, with irrigation of sugarcane fields and the expected higher food abundance there, both adult and immature individuals may attain better body condition and experience higher survival during the wet season in this habitat. The high rate of survival and high densities in sugarcane are also reflected in the lack of genetic structure of *M. natalensis* sampled across the same study area (Rohas Bonzi et al., 2019).

The populations of *Mus minutoides* and *Lemniscomys rosalia* showed different trends compared with those of *M. natalensis*. Both species had higher population densities in savanna than in sugarcane and in taller fields than shorter fields, corroborating previous studies showing that these species prefers situations with high cover (Loggins et al., 2019; Monadjem, 1999b; Monadjem and Perrin, 1997). Sugarcane fields probably represent marginal habitats for these two species that presumably use field margins and other edge habitats with adequate cover as refugia after burning of the sugarcane and for several months thereafter until the field has regained adequate cover from the next generation of growing sugarcane.

Table 5
Results of GLMM fitted to Poisson distribution for the relationship between body condition of the dominant small mammal species in sugarcane, *Mastomys natalensis*, and habitat, season and sex. Also included is the interaction between season and habitat.

	Estimate	±SE	DF	t-value	p-value
(Intercept)	−80.10	7.45	715	−10.75	<0.001
Hindfoot	4.27	0.28	715	15.14	<0.001
Season	17.70	2.98	715	5.95	<0.001
Habitat	2.58	4.18	6	0.62	0.560
Sex	3.59	0.85	715	4.23	<0.001
Season:Habitat	−5.73	2.56	715	−2.24	0.025

Shortly before harvesting sugarcane at our study site, the field is burnt, which we have demonstrated significantly affects the survival of the dominant species, *M. natalensis*, in the system. This is a surprising and unexpected finding because fire generally does not appear to affect populations of *Mastomys* species (Leirs et al., 1996b; MacFadyen et al., 2012; Yarnell et al., 2007), and has even been reported to increase their population densities (Monadjem and Perrin, 2003). This is likely because sugarcane fires do not remove all sugarcane biomass and may even result in an increase in food for small mammals in the form of dead insects. The reason for why fire has an impact on *Mastomys* survival in sugarcane fields may rest with the heat and intensity of the fire here compared with fire in native savannas. Although not measured, the temperature of fires in sugarcane fields must be significantly higher than in the neighbouring savannas based on the higher biomass available for burning in the former habitat; the flames in burning sugarcane fields typically reach many meters above the ground, visibly higher than most savanna fires in the region. Perhaps this atypical heat and intensity radiates deeper underground where *M. natalensis* presumably takes refuge in cracks, crevices, and burrows (Leirs et al., 1996b; Leirs and Verheyen, 1995). An alternative, but not mutually exclusive explanation is that these small mammals were able to survive the fire but immediately dispersed away from the burnt fields never to return, which is rather unlikely since previous work has shown that *M. natalensis* is drawn to recently burnt areas (Monadjem and Perrin, 2003).

In this study we have demonstrated that the higher density of rodents in sugarcane fields, than neighbouring savannas, is linked with a more constant survival and body condition of rodents in sugarcane throughout the year. Despite the rapidly changing physical structure of vegetation in sugarcane fields, and the intense fires at harvesting, these irrigated fields provide suitable habitat for at least one species, *M. natalensis*, a pioneer species that is well adapted for exploiting such temporally dynamic situations (Meester et al., 1979).

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