



Original investigation

Linking changes in small mammal communities to ecosystem functions in an agricultural landscape



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ABSTRACT

Global increases in agricultural production have significant implications for biodiversity and ecosystem processes. In southern Africa, sugarcane production has converted native vegetation into agricultural monocultures. We examined functional group abundance along a conservation-agriculture gradient in the Lowveld of Swaziland. We captured small mammals representing 4 functional groups: omnivores, insectivores, granivores, and herbivores and found evidence of distinct changes in small mammal functional groups across the conservation-agriculture boundary. Granivores declined with increasing distance into the sugarcane and were completely absent at 375 m from the boundary while omnivores increased in the sugarcane. Insectivores and herbivores showed no differences between the two land uses; however, during the dry season, there were significantly more insectivores at the conservation-agriculture interface than in the conservation lands. Shifts in small mammal communities have clear implications for ecosystem processes as the removal of granivores from savannah systems can drastically alter vegetative structure and potentially lead to shrub encroachment via reduced levels of seed predation, while abundant omnivorous small mammals can cause significant crop damage and increase the prevalence of vector borne diseases in the environment.

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Introduction

The global landscape is dominated by agriculture, covering more than 40% of the earth's land surface (Foley et al., 2005; Ramankutty et al., 2008; Ramankutty and Foley, 1999). In developed countries, agricultural lands often utilize intensive agricultural practices which clear native vegetation, leaving negligible amounts of natural habitats for wildlife (Krebs et al., 1999; Sotherton, 1998). As intensive agriculture practices spread throughout southern Africa and the rest of the developing world there is a growing concern that these practices will decrease wildlife diversity and subsequent ecosystem functions (Donald, 2004; Tscharntke et al., 2005). Nonetheless, the linkages among intensive agriculture, diversity

and ecosystem functioning are poorly understood (Matson et al., 1997; Tilman et al., 2002; Rands et al., 2010). Some wildlife populations appear to benefit from intensive agriculture while others may be reduced or eliminated (Matson et al., 1997; Tilman et al., 2001). Thus, there is a need to understand how differing population responses shape wildlife communities and ultimately the integrity of the ecosystem in landscapes dominated by high intensity agriculture.

One way to understand the link between communities changed by intensive agriculture and ecological processes is to measure a community's functional group structure, based on the ecological roles that species play (Clarke, 1954; Korner, 1994). Functional group structure and abundance also can be used as indicators of disturbance response and land-use impacts (Andersen, 1997a,b; Andersen et al., 2002; Jansen, 1997; Peterson et al., 1998). Furthermore, because functional groups provide a criterion that can be evaluated across taxa, their use has the added benefit of broadening the inferential space, generalizability, and comparative value of a study (Andersen, 1997a).

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During the last 40 years, large expanses (~8%) of the low-lying savanna (Lowveld) of Swaziland and southern Africa have been converted from native vegetation into areas of intensive sugarcane (*Saccharum* spp.) production (Hackel, 1993; Lankford, 2001). Sugarcane plantations combine with overgrazed communal lands and small-scale subsistence agriculture to create a matrix surrounding patches of intact vegetation that serve as *de facto* conservation areas (Monadjem and Garcelon 2005). Sugarcane production in the Swazi Lowveld has become so prolific, that the few *de facto* and designated conservation areas in the region are all adjoined by sugarcane plantations (Monadjem and Garcelon, 2005). Furthermore, from 2000–2013 the extent of sugarcane production in Swaziland increased by 28%, this trend is expected to continue (USDA, 2013).

Small mammals play an integral role within African Lowveld savanna ecosystems as herbivores, seed predators, prey items and disease vectors; changes in their community structure are likely to have consequences for the integrity and stability of the system (Goheen et al., 2004; Keesing, 2000). Nonetheless, there is only limited information on the basic ecology of small mammals in African savanna systems, few data on how small mammal communities respond to land-use alterations such as intensive agriculture, and practically no information on how small mammal community changes from intensive agriculture relate to ecosystem processes (Avenant and Cavallini, 2007; Hurst, 2010). As such, the goal of our study was to describe the changes in abundance and structure of small mammal functional groups across a spatial gradient between intensive agriculture plantations and conservation lands, and to understand how these changes might influence ecosystem functions.

Material and methods

Study area

We conducted our research in the Lowveld of Swaziland, the low-lying region between the northern Drakensburg Escarpment and the Lubombo Mountains (Fig. 1). The Lowveld lies in the eastern half of Swaziland and is its lowest, warmest, and driest region. Vegetation is characterized into 3 distinct broad-scale types: *Acacia* savanna, broadleaved woodland, and riverine forest (Mucina and Rutherford, 2006; Roques et al., 2001). Swaziland has a subtropical climate, and exhibits distinct wet (October–March) and dry (April–September) seasons; 75% and 25% of rains fall during these respective seasons (Matondo et al., 2004). Annual precipitation ranges between 550–725 mm decreasing on a north–south gradient (Matondo et al., 2005). The Lowveld is drought-prone due to the combination of erratic rain events and high summer temperatures (Matondo et al., 2004).

We conducted our research at 3 sites (Hlane-Mbuluzi, Crookes, and Nisela) where conservation lands adjoined large-scale sugarcane plantations. Conservation lands were identified as lands with an explicit goal of wildlife conservation as a component of their management. These lands included private cattle ranches, private game reserves, and national parks. Hlane-Mbuluzi included lands administered by Hlane Royal National Park, Mbuluzi Game Reserve, Tongaat-Hulett Sugar (Tabankulu Estate), and Royal Swazi Sugar Corporation (Simunye and Mhlume Estates). Conservation lands (Hlane Royal National Park and Mbuluzi Game Reserve) at Hlane-Mbuluzi were managed for wildlife conservation and tourism. Dirt and graveled access roads and a 3 m high fence separated conservation lands and sugarcane, restricting movements of medium- to large-sized mammals. Our second site (Crookes) included lands managed by Crookes Brothers Plantation and Bar J Cattle Ranch. Conservation lands were included in the Big Bend Conservancy, a consortium of land-users who managed their lands for wildlife conservation. Bar J managed their conservation lands using sustainable

stocking rates, rotational grazing, and prescribed burning. Agriculture and conservation lands were separated by dirt access roads, 1.5 m barbed wire fence and 1 m wide irrigation canals. Our third site (Nisela), was overseen by Nisela Farms where conservation lands were managed for wildlife viewing, conservation, and cattle grazing. Prescribed burning and free-range grazing were practiced here. At Nisela, agricultural and conservation lands were separated by dirt access roads, railroad tracks, and an electrified 3 m fence. Nisela used center pivot irrigation and had two structurally different varieties of sugarcane.

Sampling design

We used a gradient study design to elucidate changes in small mammal communities from conservation areas to plantation agriculture. Using ground-truthed aerial photographs and Landsat images in a GIS (ArcGIS 9.3, ESRI, Redlands, California), we digitized the linear extent of the conservation-agriculture interface at each site with the fence line between land-types representing the interface. We then placed 4 transects at random linear distances perpendicular to the interface at each site. We spaced transects >300 m apart to ensure independence of sampling units based upon estimates of small mammal (<300 g) ranges in Swaziland (Monadjem and Perrin, 1998a). Along each transect, we placed small mammal traplines at 0 (interface), 75, 150, 225, and 375 m into each land-use type, parallel to the interface (Fig. 2). We used the farthest trapline, (375 m) as a reference of the interior small mammal communities in interior of both land-uses because research suggests that the influence of the edge should be <250 m for most taxa (Ries et al., 2004). We sampled each transect once per season, and alternated sampling among the 3 sites. We duplicated our transect sampling order between the 2 seasons so that sampling events were spaced approximately 4 months apart.

Each trapline consisted of 20 Sherman live traps (size large) spaced 10 m apart ($n = 180$ traps per transect) and baited with a combination of oats and peanut butter. Our design was developed to yield high levels of area surveyed per trap. The relatively close spacing of traps and sampling for 4 consecutive nights ensured adequate sampling for small mammal species richness (Jones et al., 1996; Pearson and Ruggiero, 2003).

We placed pitfall arrays to sample for shrews at each trapline (Jones et al., 1996). Pitfall arrays consisted of 7 pitfall buckets and were offset 50 m from the Sherman live traps. They had a central pitfall with 3 10-m long, radiating drift fences set at every 120°. Additional pitfalls were placed along each drift fence at 5 m and at each terminus. Drift fences consisted of 30 cm tall plastic sheeting, staked vertically with the bottom buried; pitfalls were at least 40 cm deep to eliminate the chance of escape and were flush with the ground (Jones et al., 1996). We used 63 pitfalls (9 arrays) on each transect. We restricted pitfall trapping to one site (Hlane-Mbuluzi) during the dry season due to logistical constraints, but during the wet season all three sites were surveyed using pitfalls.

Upon capture we recorded species, age, sex, and mass of each small mammal (Kunz et al., 1996; Skinner and Chimimba, 2005). We gave each individual weighing >15 g a unique ear tag identifier (1005-1, National Band Co., Newport, Kentucky, USA), smaller individuals and African pygmy mice (*Mus minutoides*) were given ear punches (INS500075-5, Kent Scientific, Torrington, Connecticut, USA). Individuals that received ear punches were uniquely identified using a combination of measurements, including: mass, tail length, body length, and hind foot length. All captured shrews (*Crocidura* spp. and *Suncus* spp.) were collected and deposited in the Durban Natural Science Museum (South Africa) for identification. Our capture protocols and data collection followed guidelines outlined by the American Society of Mammalogists (Gannon and Sikes,

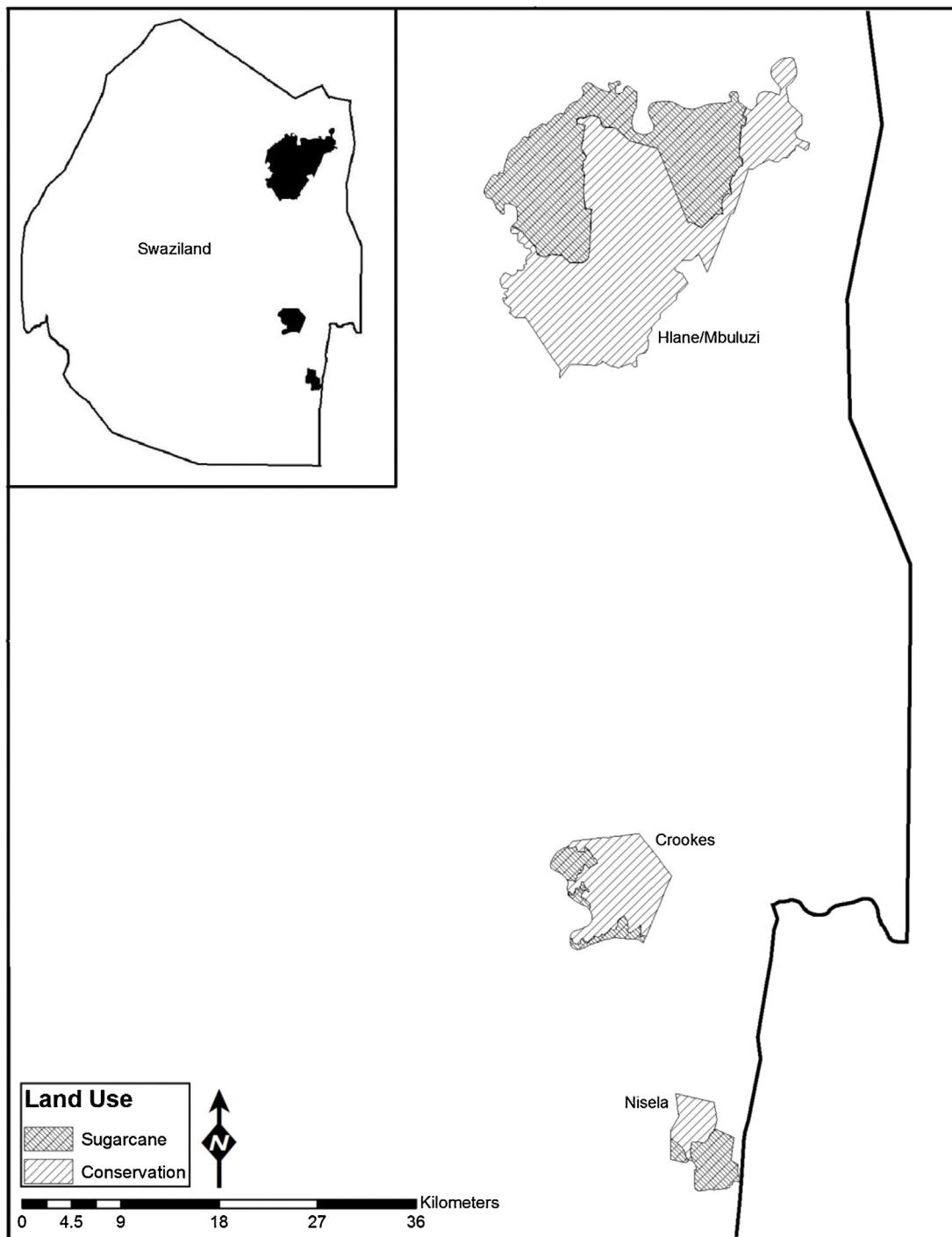


Fig. 1. Map of the 3 study sites used to examine the effects of intensive agriculture on small mammal communities in the Lowveld region of Swaziland. Interfaces are denoted by the difference between land-uses. Inset: map of Swaziland in southern Africa showing the locations of the 3 sites.

2007) and were authorized under Texas A&M University Animal Use Protocol (permit number 2008-98).

Data analysis

We analyzed our capture–recapture data using closed capture Huggins models implemented in program MARK (White and Burnham, 1999). We evaluated trap response using models (M_0 ; no variation, M_t ; time-varying, M_b ; behavioral, M_{tb} ; time-varying behavioral; Otis et al., 1978) for each species (Table A.1). Once the most parsimonious trap response model was selected based on

Akaike's Information Criteria (AIC; Burnham and Anderson, 2002), we evaluated additional models to address capture heterogeneity across land-use types (site, season, trapline location; Table A.2). We used the best fitting model for each species to estimate species abundance for each trapline by site and season.

For species with fewer captures (<50) than necessary for capture-recapture modeling, we calculated minimum number alive (MNA) estimates for each trapline by site and season (Cramer and Willig, 2005; Slade and Blair, 2000). We calculated functional group abundance by summing the individual species abundances calculated by MNA with those species whose abundances we derived

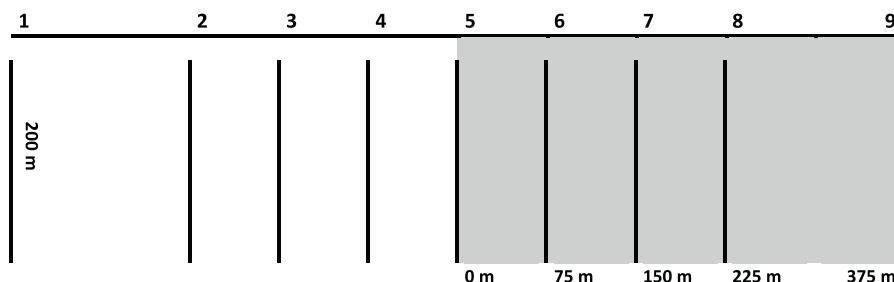


Fig. 2. Diagram of sampling design. Transects extended from conservation areas into sugarcane agriculture (gray shading). Sherman traps were placed along traplines (20 traps, 10 m apart; vertical lines). Pitfalls (circles) were placed at the origin of each trapline and offset 50 m from the Sherman traps. Traplines were placed at 0, 75, 150, 225, and 375 m into each land-use.

from closed capture Huggins analysis. For each species, we calculated its proportional abundance at each trapline for each site to provide a standard measure of the relative species response to the different land-use. We calculated proportion of abundance for each species by dividing the species abundance at each respective trapline by the total abundance for each site.

We used peer-reviewed literature (Dickman, 1995; Kerley, 1989, 1992; Leirs et al., 1995; Monadjem, 1997a; Rowe-Rowe, 1986; Skinner and Chimimba, 2005; Smithers, 1971) to determine the ratios of food groups (insects, seeds, herbage) in species diets and to classify them into functional groups (omnivore, herbivore, granivore, insectivore). We assigned species to a functional group if one food group comprised a majority (>50%) of their diet. When no food group was >50% we classified the species as an omnivore.

We examined changes in functional groups graphically and tested for differences using analysis of variance between land-uses comparing the 4 traplines (75, 150, 225, and 375 m) within the conservation land use-type to the 4 traplines at the same distance in the agricultural land-use types. We treated the 3 sites as replicates for this analysis. Additionally, we evaluated differences between each land-use type and the interface to evaluate the possibility of edge related effects (Ries et al., 2004). The unequal sample sizes encountered in these tests increased the potential for violation of the analysis of variance assumption of equal variance. We tested for unequal variances to ensure that there were not large departures from equal variance between categories; however, analysis of variance is generally robust to violation of this assumption (McGuinness, 2002). For functional groups with significant global F-tests, we performed Tukey's HSD pair-wise comparisons (Ott and Longnecker, 2010). We did not compare insectivore abundance between seasons or sites.

Results

We trapped during the dry season from 5 July to 13 October 2008 and wet season from 28 October 2008 to 10 January 2009, for 21,564 trap nights (dry season = 9648 trap nights [8640 Sherman trap; 1008 pitfall] and wet season = 11,916 trap nights [8640 Sherman trap; 3276 pitfall]). We captured 1725 unique individuals representing 13 species (Table 1). We used capture-recapture analysis (Tables A.1–A.2) to evaluate responses to intensive agriculture for 5 species (tete veld rat [*Aethomys ineptus*], single-striped grass mouse [*Lemniscomys rosalia*], Natal multimammate mouse [*Mastomys natalensis*], African pygmy mouse, fat mouse [*Steatomys pratinus*]) and for 7 species (tiny musk shrew [*Crocidura fuscomurina*], lesser red musk shrew [*Crocidura hirta*], lesser gray-brown musk shrew [*Crocidura silacea*], chestnut climbing mouse [*Dendromus mystacalis*], short-snouted sengi [*Elephantulus brachyrhynchus*], bushveld gerbil [*Gerbilliscus leucogaster*], South African pouched mouse [*Saccostomus campestris*], greater dwarf shrew [*Suncus lixus*]) we used MNA due to the sample sizes being inadequate for capture-recapture modeling. Omnivores were the most abundant

group ($n = 1204$ unique captures), followed by granivores ($n = 240$), herbivores ($n = 190$) and, insectivores ($n = 91$).

Granivores

During both seasons, granivores were more prevalent in conservation areas; with *Steatomys pratinus* not even occurring in sugarcane sites (Table 1, Figs. A.1 and A.2). There were no granivores recorded 375 m into the sugarcane and the abundance and proportional abundance for each granivore decreased with distance into the sugarcane at each site (Figs. A.1 and A.2). There were statistically significant differences between land-uses (sugarcane vs. conservation) during each season and both seasons combined (both, $p = 0.00$; wet, $p = 0.00$; dry, $p = 0.00$, Table 2). There was also a statistically significant reduction in granivores between sugarcane and the interface during the dry season ($p = 0.02$; Table 1). Within the conservation lands, granivores showed no clear trend in proportion of abundance (Figs. A.1 and A.2).

Omnivores

During the dry season omnivore abundance increased with increasing distance into the sugarcane at Hlane-Mbuluzi and Nisela, while at Crookes abundance decreased with increasing distance into the sugarcane (Table 1, Fig. A.1). During the wet season abundance increased with distance into the sugarcane at all sites (Table 1, Fig. A.1). There were significantly more omnivores in the sugarcane than conservation areas during the wet season ($F = 14.67$, $p < 0.01$) and for both seasons combined ($F = 9.01$, $p < 0.01$; Table 2).

The proportional abundance of omnivores varied by species (Fig. A.2). During the wet season, *Mastomys natalensis* increased with distance into the sugarcane. During the dry season *Mus minutoides* was most abundant near the land-use interface and during the wet season it increased with distance into the sugarcane. *D. mystacalis* ($n = 2$) was present in the farthest interior sugarcane (375 m) trapline in a natural strip of vegetation, and in the conservation land-use. *Elephantulus brachyrhynchus* ($n = 10$) was absent from the interface (0 m) and sugarcane. *Gerbilliscus leucogaster* was more abundant at each trapline in the conservation lands ($\bar{x} = 5.5$, $\sigma = 3$) than in the sugarcane ($\bar{x} = 1.8$, $\sigma = 24$) and was completely absent from the farthest interior sugarcane (Table 1).

Insectivores

During the wet season, insectivores showed no clear trend across the land-uses, but had their highest numbers within the conservation areas of Hlane-Mbuluzi and Crookes (Table 1, Fig. A.1). During the dry season, there were significantly more insectivores at interface than in the conservation lands, ($F = 4.45$, $p = 0.05$; Table 2) but there were no difference between land uses (Table 2). All of the insectivore species encountered in conservation lands were also found within the sugarcane (Table 1, Fig. A.2). However, there were

Table 1

Total unique captures of small mammal individuals by functional group and species captured at each trapline with distance (m) in parenthesis, positive (+) distances denote distances into conservation land and negative (−) into sugarcane. Trapping was conducted between July 2008 and January 2009 in the Lowveld of Swaziland.

Functional Group	Species	Trapline (distance)									Totals
		1(+375)	2(+225)	3(+150)	4(+75)	5(0)	6(−75)	7(−150)	8(−225)	9(−375)	
Omnivore	<i>Mastomys natalensis</i>	61	71	69	70	68	121	107	135	174	876
	<i>Mus minutoides</i>	25	25	25	30	37	45	36	33	25	281
	<i>Gerbilliscus leucogaster</i>	4	8	8	2	6	5	2	0	0	35
	<i>Elephantulus brachyrhynchus</i>	3	2	0	5	0	0	0	0	0	10
	<i>Dendromus mystacalis</i>	0	0	1	0	0	0	0	0	1	2
Total		93	106	103	107	111	171	145	168	200	1204
Insectivore	<i>Crocidura hirta</i>	5	10	6	9	11	4	1	4	2	52
	<i>Crocidura fuscomurina</i>	0	3	0	0	1	3	1	2	3	13
	<i>Suncus lixus</i>	6	0	1	3	1	1	0	0	0	12
	<i>Crocidura silacea</i>	0	0	0	0	0	1	0	0	1	2
Total		11	13	7	12	14	8	2	6	6	79
Granivore	<i>Aethomys ineptus</i>	23	16	15	36	21	4	2	9	0	126
	<i>Steatomys pratensis</i>	16	17	15	19	5	0	0	0	0	72
	<i>Saccostomus campestris</i>	8	6	4	7	13	1	2	1	0	42
Total		47	39	34	62	39	5	4	10	0	240
Herbivore	<i>Lemniscomys rosalia</i>	6	21	28	17	13	26	19	19	41	190
Total individuals captured		160	179	173	203	177	212	170	203	248	1725

Table 2

Results of one-way Analysis of Variance (global) test of functional group abundance by land-use (sugarcane = Agric, conservation areas = Cons) and interface (Inter) for each season and overall. Tukey's HSD pairwise tests were conducted on F-tests that were significant at or below 0.05 level. For Tukey's HSD tests adjusted p-values are reported.

Season	Functional Group	Global test		Pairwise comparison		
		df	F-value	Cons:Agric	Inter:Cons	Inter:Agric
Both	Overall	2	0.71			
	Omnivore	2	9.01	0.00	0.55	0.24
	Herbivore	2	1.93			
	Insectivore	2	0.95			
	Granivore	2	14.41	0.00	0.51	0.07
Wet	Overall	2	1.06			
	Omnivore	2	14.67	0.00	0.20	0.24
	Herbivore	2	1.5			
	Insectivore	2	1.2			
	Granivore	2	5.76	0.01	0.5	0.58
Dry	Overall	2	0.06			
	Omnivore	2	1.55			
	Herbivore	2	0.85			
	Insectivore	2	4.45	0.69	0.05	3.52
	Granivore	2	12.22	0.00	0.98	0.02

more *Crocidura fuscomurina* in the sugarcane and *Crocidura silacea* ($n=2$) was only captured within the sugarcane. Conversely, *Suncus lixus* and *Crocidura hirta* were more abundant in conservation areas ($\bar{x}=5$, $\sigma=35$) than the sugarcane ($\bar{x}=1.5$, $\sigma=1.7$), (Table 1, Fig. A.2).

Herbivores

During the dry season, *Lemniscomys rosalia* showed no clear pattern in abundance among the different sites (Table 1, Fig. A.2). During the wet season, *Lemniscomys rosalia* showed increased abundance with distance into the sugarcane at Hlane-Mbuluzi and Nisela (Table 1, Fig. A.2) and on all sites the highest or second highest abundance was recorded the furthest distance (375 m) into the sugarcane (Table 1, Fig. A.1).

Discussion

Our study showed distinct changes in small mammal populations from the interior of conservation lands to the interior

of agricultural lands. The variation in small mammal abundance relative to intensive agricultural practices differed considerably by functional group. In general, granivores decreased, omnivores increased and herbivores and insectivores showed no particular pattern across the conservation and agricultural interface.

We found that granivore abundance was significantly lower in the sugarcane, likely due to sugarcane's lack of large seeds, especially *Acacia* spp. preferred by granivorous small mammal in the region (Kerley and Erasmus, 1991; Kerley, 1992; Miller, 1994; Monadjem, 1997a). The loss, reduction and potential isolation of granivores by intensive agricultural practices seen in this study may lead to a substantial cascading effect throughout the landscape. Granivorous small mammals are important in savannah ecosystems and their removal has been shown to substantially alter vegetation communities (Bricker et al., 2010; Goheen et al., 2004; Keesing, 2000). Of particular concern is that the loss of seed predation by this functional group may contribute to the regional pattern of increased shrub encroachment that has been linked to changing wildlife communities and degraded grazing lands (Manson et al.,

2001; Weltzin et al., 1997; Moleele et al., 2002; Dirzo et al., 2007; Wright and Duber, 2001).

Conversely, omnivores increased or maintained their populations within the sugarcane. Omnivores opportunistically inhabit areas with high food availability (Monadjem, 1997b; Monadjem and Perrin, 1998a,b), thus increased abundance within the sugarcane likely reflects their ability to exploit the abundant herbaceous forage within this habitat. Additionally, by mediating natural rainfall fluctuations, irrigation of sugarcane may enable omnivores to breed earlier and more often, possibly explaining the punctuated increase in their abundance during their breeding (wet) season (Monadjem, 1998). In addition to their potential to cause significant crop damage, abundant populations of omnivorous small mammals within the sugarcane, particularly *Mastomys natalensis* and *Mus minutoides*, may have implications for humans and ecosystem integrity as these animals are known to increase the prevalence of vector borne diseases (i.e. Lassa fever, Kodoko virus) in the environment (Massawe et al., 2007; Mills and Childs, 1998; Lecompte et al., 2007; Goyens et al., 2013). Furthermore, in areas with low ground-cover or at other times of resource scarcity, sugarcane may act as refugia for these species and the diseases they carry, thus mediating fluctuations in disease prevalence and seasonality (Goyens et al., 2013).

Two insectivorous species *Crocidura silacea* and *Crocidura fuscomurina* were more common within the sugarcane, albeit in low numbers. Both species prefer moist areas (Dickman, 1995; Smithers, 1971) and it is possible that irrigation plays a role in these species to persistence in dry Lowveld savanna environments. However, overall we did not see increased numbers of insectivores in the sugarcane (Getz, 1961; McCay and Storm, 1997). The lone herbivore *Lemniscomys rosalia* did not show a consistent response across the land uses but appeared to select for sugarcane when the adjoining lands had low cover (Hlane-Mbuluzi and Nisela; Hurst, 2010). This trend is corroborated by previous research showing that species avoid or tend to avoid areas with low grass cover (Monadjem, 1997b; Monadjem and Perrin, 1998a; Yarnell et al., 2007).

Conclusion

As the prevalence of intensive agricultural practices increase in the developing world, there are clearly consequences for wildlife communities. It is becoming evident that alterations to wildlife communities have real implications for ecosystem integrity and processes (Matson et al., 1997; Tilman et al., 2002; Rands et al., 2010; Flynn et al., 2009). In our study, we saw a drastic reduction in populations of granivorous small mammals, that help maintain savannah systems, and increases in the omnivorous species, that have been linked to crop damage and disease outbreaks. Accordingly, there is a need to promote more holistic approaches to agricultural production that do not sacrifice ecosystem functions. One potential solution may be to create structurally complex agricultural landscapes that retain or restore some natural habitat features and promote connectivity within the mosaic. This type of approach should help mitigate stressors on wildlife communities and maintain the functionality necessary for healthy ecosystems (Lacher et al., 1999; Tscharntke et al., 2005; Yapp et al., 2010; Tscharntke et al., 2008).

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.mambio.2013.08.008>.

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