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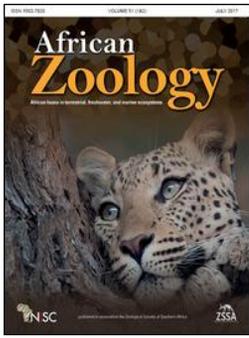
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Changes in bat community composition and activity patterns across a conservation-agriculture boundary

Fezile Mtsetfwa^{1,2*}, Robert A McCleery¹ and Ara Monadjem^{1,2,3}

¹ Department of Wildlife Ecology and Conservation, School of Natural Resource and Environment, University of Florida, Florida, United States

² Department of Biological Sciences, University of eSwatini, Kwaluseni, eSwatini

³ Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa

*Corresponding author, e-mail: fezile@ufl.edu

Agricultural landscapes are typically associated with a decreased biodiversity, particularly when they extend across large spatial scales. Despite the fact that some African bat species seem to provide essential ecosystem services across landscapes, we only have a limited understanding of how intensive agricultural practices influence bat communities. This study investigated the effects of sugarcane monoculture on the composition of both bat species and functional groups across a conservation-agricultural matrix. Specifically, we wanted to understand changes in the bat communities within savannas and sugarcane plantations. We categorised bats into broad foraging (functional) groups based on their echolocation call structure: open-air; clutter-edge; and, clutter. To measure bat activity, we established twelve 25 ha grids randomly located in savanna and sugarcane vegetation. Within each grid we placed nine acoustic detectors, in 3 × 3 formation, 250 m apart; totalling 54 plots in each land use. We sampled each plot over four nights (two in the wet season and two in the dry season) during a one-year period. We did not observe a significant difference in species richness between savanna and sugarcane. However, there was a difference in functional group composition. Sugarcane negatively affected clutter foragers; this group was practically absent here despite occurring within neighbouring savannas. We observed distinct patterns of seasonality in bat activity, with activity of all functional groups being reduced in the dry season.

Keywords: biodiversity, Chiroptera, echolocation, savanna, seasonality, species richness, sugarcane

Introduction

Agricultural intensification is thought to be a major driver of species loss and population declines in bats across the globe (Park 2015). In Britain alone, agricultural intensification and habitat loss have been identified as the reason for the decline in six out of 16 bat species (Wickramasinghe et al. 2003). However, this pattern is not universal and some insectivorous bat communities might respond differently to agricultural intensification (Willig et al. 2007; Heim et al. 2016; Kelly et al. 2016). For example, recent studies have shown that species richness of insectivorous bats is not significantly influenced by agricultural intensification, but that the relative abundance of forest-adapted species was negatively impacted (Freudmann et al. 2015; Cleary et al. 2016; Heim et al. 2016). Other studies have shown that some species increase their activity over agricultural fields, compared with areas of native vegetation (Rogers et al. 2006; Williams-Guillen and Perfecto 2011; Noer et al. 2012).

Insectivorous bats are effective bioindicators (Jones et al. 2009) and provide the critical ecosystem service of suppressing agricultural pests (Kunz et al. 2011; Puig-Montserrat et al. 2015; Maas et al. 2016; Librán-Embid et al. 2017). Insect abundances in agricultural fields have been linked to increased bat activity (Taylor et al. 2013; Bader et al. 2015), and bats are known to feed on agricultural pests (Bohmann et al. 2011; Aizpurua et al. 2018). The

average economic value of bats for the American agricultural industry is estimated to be US\$22.9 billion (Boyles et al. 2011). A recent study on the importance of bats to the macadamia industry in South Africa estimated avoided costs at US\$1.4 to US\$3.4 million per year (Taylor et al. 2018).

In southern Africa, the conversion of lowland savannas from native vegetation to sugarcane monocultures has been expanding (Hackel 1999; Lankford et al. 2001). This expansion has had significant impacts on terrestrial small mammal communities by increasing the populations of generalists that thrive in sugarcane fields and restricting specialists to fragments of native vegetation (Hurst et al. 2013; Hurst et al. 2014). However, the impact of sugarcane plantations on bat communities remains poorly understood.

Wing morphology and echolocation call design are two of the most fundamental features that determine habitat use and foraging behavior by bats (Schnitzler and Kalko 2001). This has led to bats being classified into the following functional groups (Denzinger and Schnitzler 2013): open-air foragers (e.g. families Molossidae and Emballonuridae) with quasi-constant frequency (QCF) calls and long, narrow wings; clutter-edge foragers (e.g. Vespertilionidae and Miniopteridae) with frequency modulated (FM) calls and broader wings; and clutter foragers (e.g. Hipposideridae and Rhinolophidae) with

constant frequency (CF) calls and the broadest wings (Monadjem et al. 2010; Taylor et al. 2013). It is the open-air foragers with long, narrow wings and QCF calls that are typically associated with agricultural fields and other open habitats (Monadjem et al. 2010).

We are unaware of community-wide investigations of bats in sugarcane; however, in one African study open-air foragers (of the family Molossidae) preferred to forage in sugarcane fields rather than in neighbouring native savannas (Noer et al. 2012). Similar observations have been made in coffee plantations in the Neotropics, where the activity of open-air foragers increased over agriculturally intensified areas (Williams-Guillen and Perfecto 2011). The increased activity of some bat species in agricultural monocultures demonstrates their potential as pest control agents (Boyles et al. 2011; Taylor et al. 2013; Wanger et al. 2014), but it might also be indicative of increased generalists at the expense of specialist species and overall bat species diversity (Monadjem and Reside 2008). Hence, understanding the interplay between intensive agricultural land use and the bat communities that they support will have important economic and conservation consequences.

We examined the impact of land use (sugarcane plantation vs native savanna) on the bat community diversity and function in Swaziland. Bat diversity is high in this region where more than 30 species have been recorded to date (Monadjem and Reside 2008; Shapiro and Monadjem 2016). Our specific objectives were to: 1) ascertain whether bat activity and species richness differed in sugarcane and native savanna; and 2) compare the foraging (functional) group composition between the two land uses. We expected bat activity to be greater in sugarcane, but species richness to be greater in savanna. Furthermore, we expected open-air foragers to predominate in sugarcane, with a more even distribution of the three foraging groups in savanna.

Materials and methods

Study area

The study area was located in north-eastern Swaziland, in sugarcane fields belonging to the Royal Swaziland Sugar Cooperation (RSSC) and Tongaat Hulett, and adjoining savannas in Mlawula Nature Reserve, Mbuluzi Game Reserve, and Hlane Royal National Park (Figure 1). Commercial (irrigated) sugarcane plantations consist of about a quarter of the land cover type in this region, the rest being rain-fed agricultural fields, urban centers, and protected areas (Bailey et al. 2016). The area has a subtropical climate with hot, wet summers and dry, cool winters. Mean monthly temperatures for January and July are 26 °C and 18 °C, respectively, whereas mean annual rainfall ranges from 550 to 725 mm (Monadjem and Reside 2008). The native vegetation of this area is classified as microphyllous savanna with patches of riparian forest occurring along rivers and major drainage lines (Roques et al. 2001). A recent study characterised shrub cover in this region that suffers from bush encroachment, with certain sites reaching 58% cover at a broad scale and 95% cover at a local scale (McCleery et al. 2018).

Data collection

We recorded bat activity on 12 grids each measuring 25 ha (Figure 1). We located these grids randomly in savanna (six grids) and sugarcane (six grids), using the Create Random Points sampling tool in ArcGIS 10.1 (ESRI, 2011). We established nine plots (250 m apart) in each grid in a 3 × 3 formation at which Anabat II and Anabat Express bat detectors (Titley Scientific, Ballina, NSW, Australia) were placed. We marked the centre of each plot with a Garmin 72H Global Positioning System. We fixed a single bat detector at each plot, and recorded bat calls over four nights, two in the wet season (January to February 2015) and two in dry season (June-August 2014). The detectors were placed out before sunset and retrieved the following morning after sunrise, for a total of 432 sampling nights. We attached bat detectors to poles 2 to 4 m above the ground, to ensure that the detectors were situated above the height of the growing sugarcane.

Data preparation

Data from the bat detectors were downloaded using the program CF Read (for those recorded with Anabat II) and Analook W (for those recorded with Anabat Express). We used a general anti-noise filter (Chris Corben, <http://www.hoarybat.com>) to identify and remove those files with only noise. The anti-noise filter was conservative, removing most noise files and no bat calls. The remaining noise files were scanned and removed manually. The files that “passed filter” were then manually examined for bat calls.

An automated call identification system based on the bats present in the study area (Monadjem et al. 2017) was used to identify bat calls. This automated identification system uses the in-built scan function in Analook W to read sonograms. Complete separation of different bat species with overlapping call parameters (such as peak frequency or duration of the call) is often impossible in African savannas (Taylor et al. 2013; Monadjem et al. 2017), and elsewhere in the world (e.g. Kalda et al. 2015; Heim et al. 2016; Toffoli and Rughetti 2017; Russo et al. 2018). For those species with overlapping call parameters, identification was made to a group of closely related species or to family level. We calculated activity as the number of minutes in one night with at least one bat call for each species (Miller 2001), which we refer to as “uncorrected calls” hereafter (see below for the definition of “corrected calls”). Our filters and scans were unable to extract the calls of *Myotis* and *Rhinolophus* spp. and other species that might have been missed by the filters, consequently we manually scanned for calls.

To resolve overlapping species call parameters, we combined *Chaerephon pumilus* and *Mops condylurus* (family Molossidae) into a single group. There was also significant overlap in the calls of Vespertilionidae bats, with *Neoromicia nana* and *Scotophilus dinganii* being the only two species whose calls could be distinguished with certainty in this family. All other vespers recorded in this region (*Neoromicia zuluensis*, *Scotophilus viridis*, *Pipistrellus hesperidus*, and *Nycticeinops schlieffeni*) (Monadjem and Reside 2008) were combined into a group labeled “other vespers”. Similarly, Rhinolophidae bats (*Rhinolophus darlingi*, *R. simulator* and *R. blasii*) were

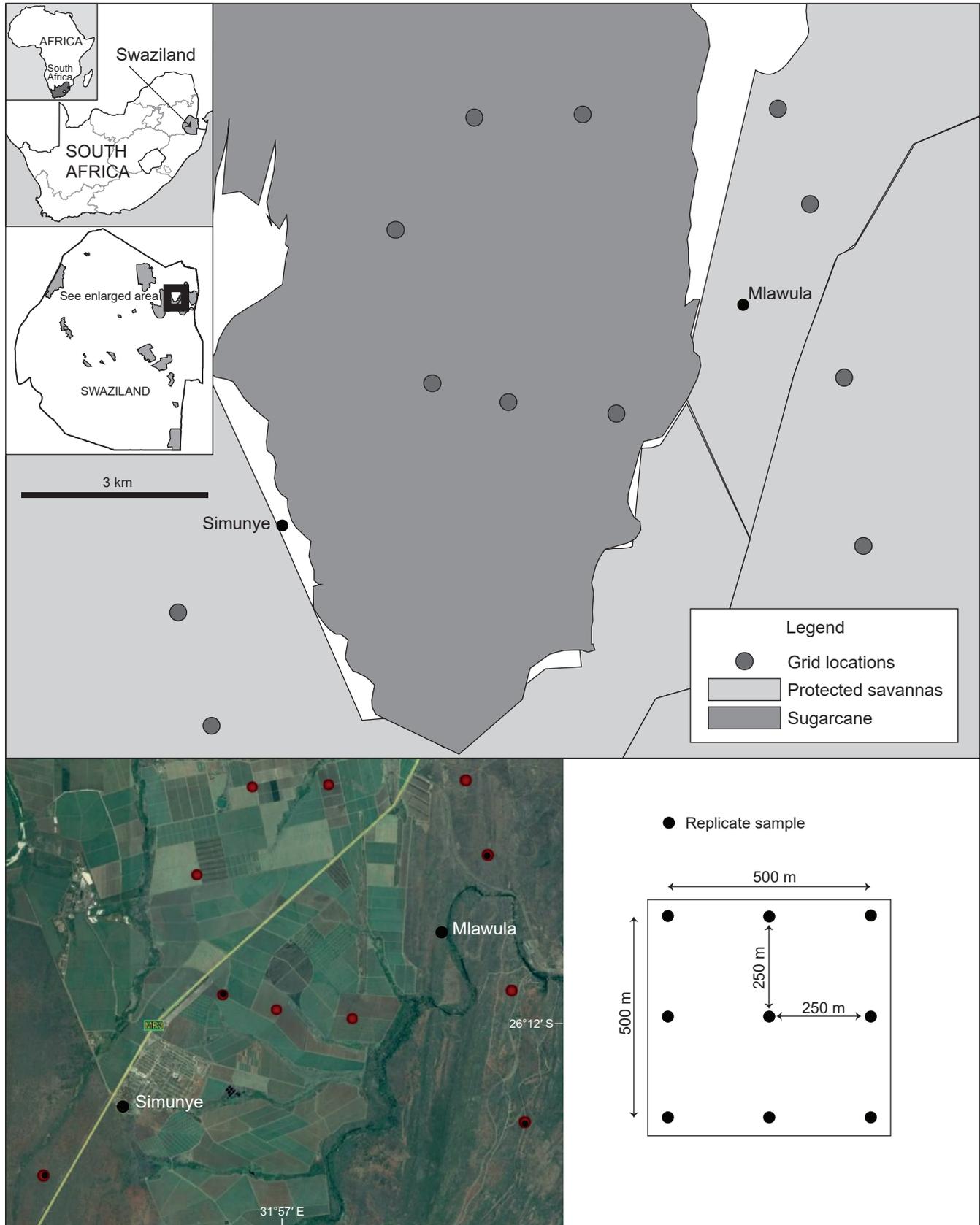


Figure 1: Study area showing sampling sites in sugarcane and savanna land uses in north-eastern Swaziland where acoustic surveys were conducted for insectivorous bats. The insert on the bottom left shows the arrangement of replicate samples within each of the 12 grids.

only identified to genus level (*Rhinolophus* spp.) because of similarity of the calls of these species in the region (Monadjem et al. 2007).

Different species of bats call at different intensities (Jakobsen et al. 2013), resulting in different distances at which they can be detected with a bat detector (Monadjem et al. 2017). We corrected bat activity by accounting for differences in detection distances by applying conversion factors as follows: open-air foragers = $\times 0.000344$, clutter-edge foragers = $\times 0.002648$, clutter foragers = $\times 0.063900$ (based on Monadjem et al. 2017). The functional group correction factors were obtained by calculating the mean detection distance for all species constituting each group in the study area as presented in Monadjem et al. (2017). These are referred to as “corrected calls” hereafter (by which we mean corrected for detection distance).

Statistical analyses

To determine whether total bat activity and species richness (our two response variables) were influenced by season (wet vs dry) and land use (savanna vs sugarcane), we used generalised linear mixed models (GLMM) using the Package lme4 (Bates et al. 2015) in the program R version 3.3.3 (R Core Team, 2017). Specifically, we evaluated a suite of competing models that looked at individual effects of land use (savanna vs sugarcane) and season (wet vs dry), plus their additive and interactive effects (Tables 1 and 2). After evaluating the distribution of our data, we fitted species richness to a Gaussian distribution and total bat activity to a Poisson distribution. We set grid as a random effect to address spatial autocorrelation. Additionally, we assessed whether there was any difference in bat activity response to land use and season by functional group (open-air, clutter-edge and clutter foragers). To do this we ran GLMM models predicting bat activity on “corrected calls” of each functional group by land use, season, and their additive and interactive effects (Table 1). In all models, bat activity was set to a Poisson distribution and grid as a random effect. We evaluated all models based on their Akaike’s Information Criterion (AIC) values obtained through the AICtab function in the R package AICcmodavg (Mazerolle, 2017) and considered all models within 2 AIC points of the top model as competing models. We evaluated beta estimates of variables at 95% confidence intervals (CI) in competing models and considered those that did not include 0 to be relevant. If categorical variables were relevant, we examined them further by plotting the 95% CI and beta estimate of each category. Finally, we determined the magnitude of change in predicted bat activity and

richness across different seasons and habitats using the predictSE function.

Results

General

We recorded a total of 18 036 calls from the 108 plots in savanna and sugarcane, comprising five different families of bats. We identified five individual species, as well as an additional three species groups, consisting of 2 to 4 species per group (Table 3). All species and species groups were recorded in both the savanna and sugarcane sites, but detection rates varied. For example, *Taphozous mauritanus*, all the molossids and *Scotophilus dinganii* were recorded more frequently in the sugarcane, whereas *Miniopterus natalensis*, “other vespers” and *Rhinolophus* spp. were more frequently recorded in savanna (Table 3).

Overall, the most frequently recorded species or species group was the *Chaerephon pumilus/Mops condylurus* group that accounted for half (49.8%) of the uncorrected

Table 2: Candidate models used to determine effects of land use and season on species richness

Model name	Species richness	
	dAIC	df
Season \times Land use	0.0	6
Season + Land use	0.4	5
Season	5.8	4
Land use	127.1	4
Intercept	128.6	3

Table 3: Summary of the uncorrected bat activity by species and species groups recorded in savanna and sugarcane sites in north-eastern Swaziland

	Species/Group	Savanna	Sugarcane
Emballonuridae	<i>Taphozous mauritanus</i>	284	1 001
Miniopteridae	<i>Miniopterus natalensis</i>	148	63
Molossidae	<i>Chaerephon pumilus/</i>	2 783	6 308
	<i>Mops condylurus</i>		
	<i>Mops midas</i>		
Vespertilionidae	<i>Neoromicia nana</i>	38	67
	<i>Scotophilus dinganii</i>	1 605	3 384
	“Other vespers”	1 448	667
Rhinolophidae	<i>Rhinolophus</i> spp	110	15
	Total	6 510	11 751

Table 1: Candidate models used to determine effects of land use and season on total bat activity and on functional groups (open-air, clutter-edge and clutter foragers). The delta AIC (dAIC) is the difference in AIC units between each candidate model and the top model

Model name	Total Activity		Open-air		Edge		Clutter	
	dAIC	df	dAIC	df	dAIC	df	dAIC	df
Season \times Land use	0.0	5	0.0	5	0.0	5	0.0	5
Season	6 617.0	4	544.8	4	1 941.9	4	32 037.1	4
Season + Land use	6 619.0	3	536.3	3	1 941.7	3	32 039.0	3
Land use	162 698.9	3	21 528.0	3	118 764.0	3	54 732.3	3
Intercept	162 696.9	2	21 536.5	2	118 764.2	2	54 730.4	2

calls; this was followed by *Scotophilus dinganii* that accounted for more than a quarter (27.3%). Based on uncorrected calls, the sequence of bat families (based on the percentage of total uncorrected calls accounted for by each family) from most to least abundant was: Molossidae (51.6%), Vespertilionidae (39.5%), Emballonuridae (7.0%), Miniopteridae (1.2%), and Rhinolophidae (0.7%).

Species richness

Species richness was best described by a model with an interaction between season and land use. However, the model with an additive term for the two variables was also within 2 AIC units of the best model. These two models were therefore competing (Table 2). Within the best model, only season was a relevant variable ($\beta = -2.02$, CI: $-2.47 - -1.56$). In the “dry” season, bat species richness was reduced in both the savanna and sugarcane habitat (Figure 2). Land use

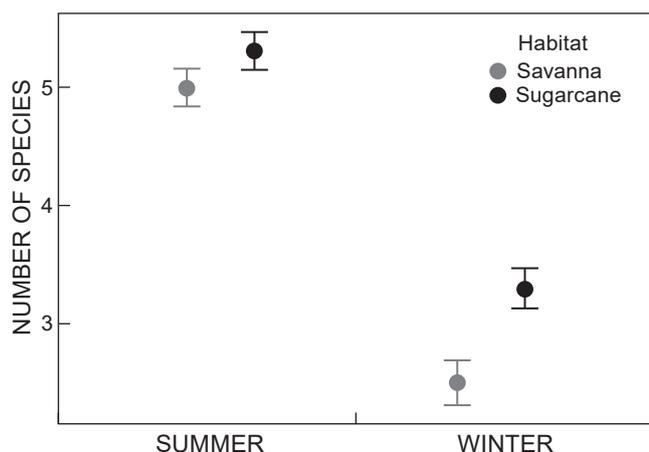


Figure 2: Beta coefficients of land use and season interactions at the 95% CIs for species richness.

alone was not a relevant variable ($\beta = -0.31$, CI: $-0.75 - 0.12$) for predicting species richness and neither was the interaction between land use and season ($\beta = -0.52$, CI: $-1.18 - 0.133$).

The competing model corroborated the effect of season as a relevant variable ($\beta = -2.26$, CI: $-2.59 - -1.93$) in reducing species richness across both the savanna and sugarcane land uses during the “dry” season. It also showed land use to be a relevant variable ($\beta = -0.54$, CI: $-0.87 - -0.22$). Species richness was reduced in the savanna.

Total bat activity

The top and only competing model for total bat activity was a model with an interaction term between season and land use (Table 1). Within this model, season ($\beta = -1.27$, CI: $-1.28 - -1.25$) was a relevant variable with activity decreasing during the “dry” season (Figure 3a) whereas land use was not ($\beta = 0.13$, CI: $-0.38 - 0.63$). We also found that the interactive effect of season and land use ($\beta = -0.80$, CI: $-0.82 - -0.78$) was a relevant predictor of total bat activity with decreased bat activity in the “savanna” during the “dry” season (Figure 4a).

Activity of foraging groups

Functional groups had varying responses to the effects of land use and season (Figure 3).

The best models explaining activity of open-air and clutter-edge foragers activity, was a model with an interaction term between season and land use for both foraging groups (Table 1). Within the best model for clutter-edge foragers, season ($\beta = -1.62$, CI: $-1.71 - -1.54$) was a relevant variable with activity decreasing during the “dry” season whereas land use was not ($\beta = -0.21$, CI: $-0.59 - 0.18$). We also found that the interactive effect of season and land use ($\beta = -0.61$, CI: $-0.75 - -0.46$) was a relevant predictor of clutter-edge activity, with decreased bat activity in the “savanna” during the “dry” season (Figure 4b).

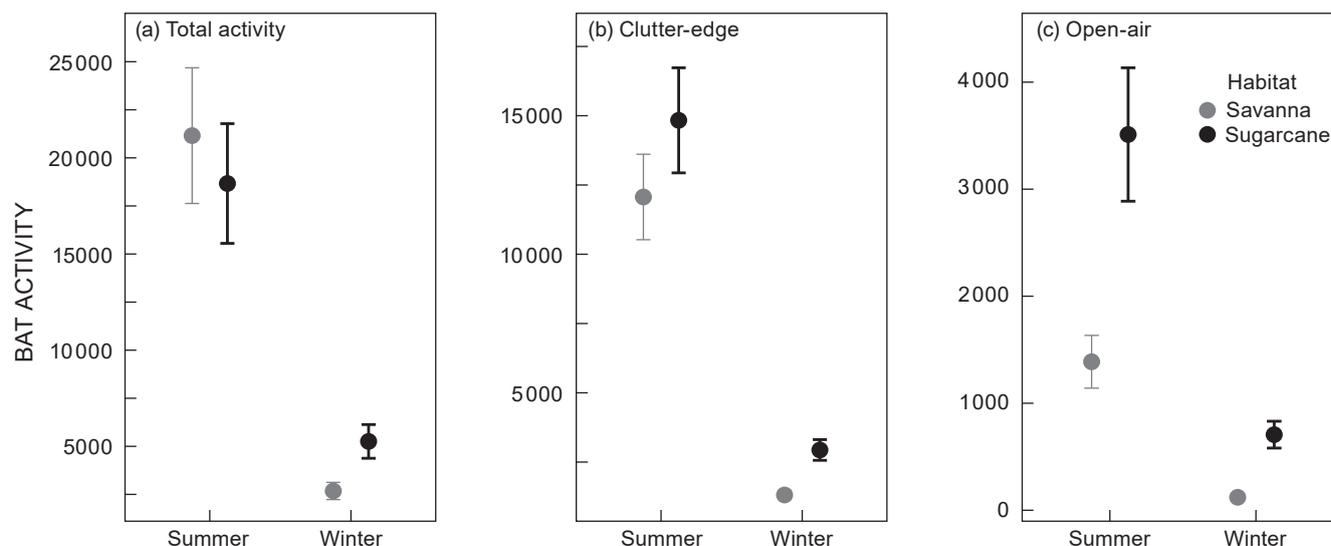


Figure 3: Predicted mean bat activity (\pm SE) estimated from the “corrected bat calls” in savanna and sugarcane land uses in north-eastern Swaziland.

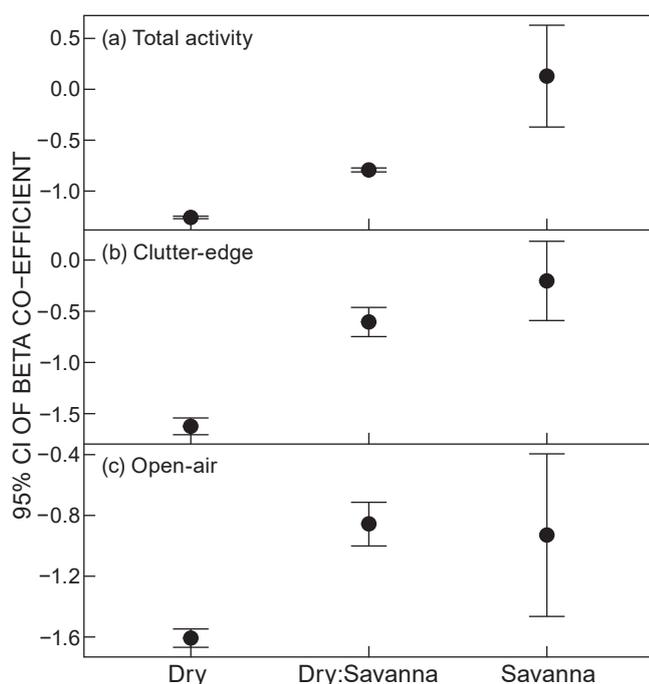


Figure 4: Beta coefficients of land use and season interactions at the 95% CIs for Total bat activity (a), activity of clutter-edge (b) and open-air (c) functional groups estimated from the “corrected bat calls”.

For the model best predicting open-air foraging activity, all variables were relevant. The “dry” season resulted in the highest reduction of bat activity ($\beta = -1.61$, CI: $-1.68 - -1.54$), whereas the effects resulting from land use alone ($\beta = -0.93$, CI: $-1.46 - -0.39$) and that from the interaction of land use and season ($\beta = -0.85$, CI: $-1.00 - -0.71$) had reduced effects on open-air foragers’ activity. There was no difference between the effect caused by season alone and that caused by the interaction of season and land use, because these two variables had overlapping confidence intervals (Figure 4c).

The model with an interaction term between season and land use failed to converge for the clutter functional group, because one of the categories had no detections; no clutter foragers were recorded in the sugarcane in the wet season. We were therefore unable to model the effects of the interaction between land use and season on the activity of clutter foragers from the GLMM analyses. However, by looking at the response of individual effects, we could determine that the “dry” season had a negative influence on the number of clutter foragers recorded. There was no statistically significant difference in the activity of clutter species between the two land uses. However, *Rhinolophus* spp. were seven times more active in the savanna plots compared with those in sugarcane (Table 3).

Discussion

We assessed the impact of sugarcane monocultures on the activity of bat assemblages in an African savanna mosaic landscape. Our results suggest that such monocultures do not have a major effect on species richness of bats in

this region. The relationship between species richness and land use varies across geographical regions and bat assemblages. For example, oil palm plantations in the Neotropics have been shown to negatively impact bat species richness of the family Phyllostomidae (Freudmann et al. 2015). A similar decline in species richness has been reported for bats in rice paddies in Costa Rica (Heim et al. 2016) whereas pineapple plantations in the same country were not found to have a significant impact on species composition (Cleary et al. 2016). Hence, the type of agriculture and the bat community in question could be driving factors in such studies.

A different conclusion is reached when examining the effects of agriculture on bat species composition. Our study corroborates the findings of other researchers that have demonstrated that agricultural systems result in modified bat species assemblages, typically where open-air foragers dominate the altered landscapes (Wickramasinghe et al. 2003; Park 2015; Heim et al. 2016; Toffoli et al. 2017).

Our findings on the activity patterns of open-air foragers are consistent with results of a telemetry study of *Chaerephon pumilus*, and *Mops condylurus* (family Molossidae), which showed that these species selectively foraged over sugarcane and reduced their activity over savannas (Noer et al. 2012). Being generalists (Monadjem et al. 2010), these species are highly adaptable to changes that occur in their habitat. Open-air foragers are known to increase their activity over open agricultural landscapes (Freudmann et al. 2015; Heim et al. 2016). A sudden increase in their numbers could also be viewed as an indication of habitat disturbance, and sugarcane plantations have been found to promote the occurrence of generalist species of other mammalian taxa (Hurst et al. 2013).

Clutter foragers were, from an ecological perspective, completely absent from sugarcane. Within this foraging group, we recorded only the genus *Rhinolophus*, which is extremely sensitive to habitat alteration, typically disappearing from farms with even low levels of agricultural practice (Russo et al. 2002; Russo and Jones, 2003; Toffoli and Rughetti, 2017). When clutter foragers are recorded in agricultural landscapes, their activity is often reduced in comparison to other functional groups (Heim et al. 2016). It is clear that this functional group is seriously affected by sugarcane monocultures that could have important ecological consequences (Kunz et al. 2011), but the exact nature of these consequences has yet to be determined. By gleaning prey off plants or the ground, clutter bats forage in a very different manner from open-air or clutter-edge foragers that typically take prey in the air (Monadjem et al. 2010). How the removal of gleaning bats might affect pest insects is not yet known.

Our study was limited by the inability to distinguish between all bat species in our system, a common problem encountered in studies that record bat activity with ultrasonic detectors (Taylor et al. 2013; Heim et al. 2016; Russo et al. 2018). We suggest that future studies carefully examine the similarity in species richness between native savannas and sugarcane plantations that we report in this study, because this might be an artefact of not being able to distinguish calls to species level. Our Anabat detectors might have also been limited in recording all echolocating bat species; for example, the low intensity calls of *Nycteris thebaica* are generally not

obtainable (Monadjem et al. 2017), yet this species is known to occur in the study area (Monadjem 1998; Monadjem and Reside 2008). Nonetheless other studies have observed that natural habitats best conserve bat species diversity, particularly as patches within agricultural landscapes (Kalda et al. 2015; Kelly et al. 2016). Furthermore, low-lying savannas in Swaziland have been shown to harbour a diverse bat fauna (Monadjem and Reside 2008). Our findings have demonstrated the importance of native savannas for the persistence of an entire functional group (clutter foragers). Preserving native habitats within agricultural landscapes improves bat diversity (Kalda et al. 2015; Kelly et al. 2016), as does having unmodified forests in close proximity to agricultural landscapes (Freudmann et al. 2015; Cleary et al. 2016). The conversion of native savannas to sugarcane plantations is a growing trend in southern African savannas (Bailey et al. 2016). Where these conversions are inevitable we recommend leaving small patches of savanna within fields to promote the activity of some cover-dependent gleaning bat species, otherwise we advocate for the conservation of native savannas where optimal biodiversity can be conserved.

Conclusions

We present the first study that looks at impacts of any African crop monoculture on bat activity. Our study demonstrated that native savannas conserve optimal functional bat diversity. Although bat species found in savannas and sugarcane are similar, the assemblages dominating each habitat are markedly different. *Taphozous mauritianus*, all the molossids and *Scotophilus dinganii* (i.e. open-air and clutter-edge foragers) predominate in sugarcane fields, whereas *Miniopterus natalensis*, “other vespers” and *Rhinolophus* spp. (clutter-edge and clutter foragers) are more active in savannas. These findings underscore the impact of sugarcane monoculture on bat assemblages typically associated with savanna habitats. Our findings suggest that the continued conversion of savannas to sugarcane will result in the loss of ecological services provided by clutter foragers. On the other hand, the increased activity of open-air and clutter-edge foragers over sugarcane plantations provides additional evidence that bat species in these functional groups might be utilised to suppress populations of insect pests in this agricultural system. The dry season moderates the activity of all functional groups across savanna and sugarcane land uses.

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