



Research article

Influence of sugarcane growth stages on bird diversity and community structure in an agricultural-savanna environment

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ABSTRACT

Agricultural intensification is a threat to terrestrial ecosystems around the world. Agricultural areas, especially monocultures, create homogenous landscapes for wildlife. However, certain crops, such as sugarcane, are harvested in phases, creating a mosaic of fields in different stages of growth. We investigated changes in avian communities across four different sugarcane growth stages: emerging, short, medium and tall sugarcane, as well as control sites that represented native savanna habitat in northeast Eswatini prior to conversion to agriculture. In total, we sampled nine sites in sugarcane fields (at different growth stages) and three in native savanna. We conducted bird counts at 5-week intervals along 200m line transects over both the breeding and non-breeding seasons. We recorded a total of 124 bird species belonging to 58 families. Bird species richness and diversity were higher in savannas compared to any stages of growth in sugarcane. In contrast, functional beta diversity and uniqueness were higher in sugarcane than in savanna. Community composition was also different between the two land-uses. While there was overlap in bird species composition between different sugarcane growth stages, there was high beta diversity and high turnover between sites, indicative of the high temporal and spatial variability in bird communities in sugarcane fields. We demonstrated that the spatial and temporal variability created by the different growth stages of sugarcane promotes the occurrence of species with different traits, which may contribute to ecosystem functioning and promote the conservation of bird species as sugarcane fields can provide resource complementation for species with different needs.

1. Introduction

The expansion and intensification of agriculture is one of the principal threats to biodiversity, especially in tropical and sub-tropical regions of the world (Foley et al., 2005; Laurance et al., 2013). Crop agriculture typically involves clearing native vegetation (Matson et al., 1997), which homogenizes the environment both in terms of fine-scale vegetation structure and broad-scale variation across landscapes (Altieri, 1999). Recent studies have demonstrated that homogenization of vegetation structure in African savannas results in the decline of species diversity (Ke et al., 2018; McCleery et al., 2018)

and changes the distribution of feeding guilds (Azman et al., 2011; Gray et al., 2019).

Despite the significant alterations that agriculture entails, such areas are increasingly recognized as important components of landscapes that may still provide habitat or resources for some species (Gayer et al., 2019; Tschamtkke et al., 2005). However, one aspect of agricultural systems that has been largely overlooked is the inherent spatial and temporal variability of cropping (Vasseur et al., 2013). This variability is typically introduced by agricultural management that includes sowing, planting, harvest of crops, or ploughing of the soil (Gheler-Costa et al., 2013), which creates different structural variation across crop fields (spatial heterogeneity) or over time (temporal heterogeneity) in the same

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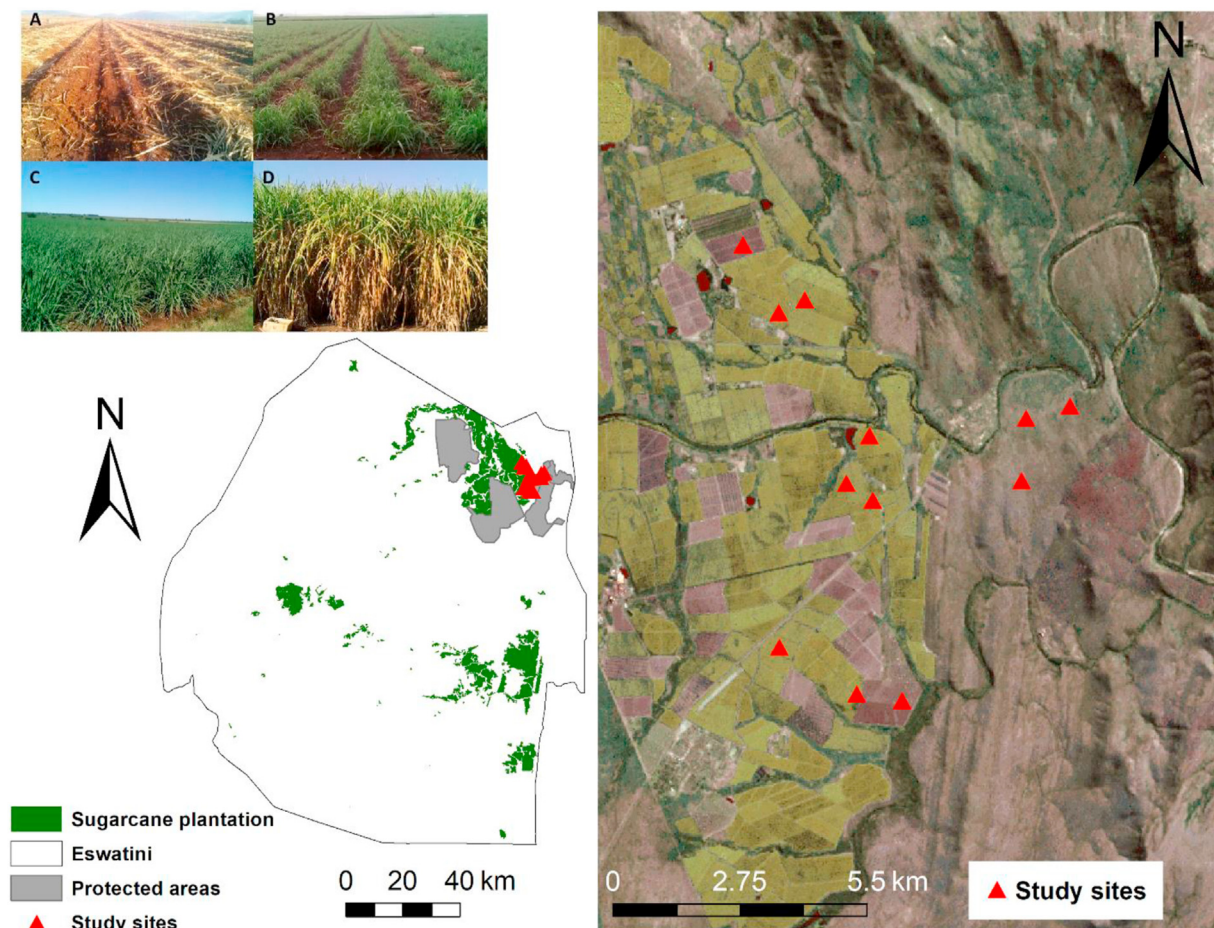


Figure 1. Map of Eswatini showing the sampling sites in the savanna (protected areas in grey) and sugarcane plantations (green). Red triangles represent the twelve sites surveyed: nine in the sugarcane and three in savanna. Photos show the four different growth stages from A–D: emerging, short, medium, and tall sugarcane, respectively.

field. Hence, agricultural areas are best considered as a mosaic of different crops, crops at different stages of growth, fallow fields, or crops together with remnant patches of native vegetation.

One of the major cash crops grown in tropical and subtropical Africa is sugarcane, which is often cultivated in large commercial monoculture plantations (Kalinda and Chisanga, 2014). Commercial sugarcane plantations tend to favour generalist species, while specialists often do not persist, thus reducing biodiversity (Hurst et al., 2013; Reynolds et al., 2018; Smith et al., 2015). While this highlights the broad-scale effects of agricultural landscapes, there is still limited information regarding how heterogeneity within a particular farm or plantation may alter these outcomes (Mamba et al., 2019). In southern Africa, as in other tropical and subtropical countries such as Brazil and India, sugarcane has a long growing season lasting roughly ten months from planting to harvest. Because individual fields are planted at different times, each ostensibly homogeneous sugarcane plantation is, in fact, a mosaic of sugarcane at different growth stages and as such presents different fine-scale vegetation structure. Understanding how ecological communities respond to this heterogeneity is important for informing conservation management in such commercial agro-ecosystems yet studies looking at this effect are lacking.

Birds are a valuable taxonomic group as bio-indicators (Lawton et al., 1998; Ndagang'a et al., 2013) that also reflect changes in other components of biodiversity (Schulze et al., 2004; Skowno and Bond, 2003). Bird community structure is closely tied to physiognomic attributes of the vegetation and there are well known relationships between species richness and structural diversity of the habitat which is important to birds

(MacArthur and MacArthur, 1961; Macnally, 1990; Monadjem and Virani, 2016; Tu et al., 2020; Wiens and Rotenberry, 1981), as well as other taxa (McCleery et al., 2018; Rivera-Pedroza et al., 2019; Thompson and Gese, 2013; Verdú et al., 2011). In addition, birds provide a wide range of important ecosystem services, such as pest control and pollination (Chain-Guadarrama et al., 2019; Sekercioglu, 2006).

Phenotypic traits of species play a critical role in determining their contribution to ecosystem services and functioning (Clare et al., 2016; Norberg et al., 2001; Tilman, 2001). Functional diversity describes the variation of these traits (Mason et al., 2005; Tilman, 2001), and may, therefore, be useful for understanding how their persistence or loss may affect ecosystem-level processes (Petchey and Gaston, 2006). Likewise, beta diversity, the change in diversity across sites or over time, may provide insights into the interactions of abiotic and biotic factors in shaping species communities (Hu et al., 2018; Si et al., 2015). Although beta diversity has traditionally been studied across spatial dimensions (Legendre and Condit, 2019), it can also be applied to changes of species in the same area over time (Barton et al., 2013). Bird communities, in particular, vary substantially over both time and space (Sekercioglu, 2012), and understanding how this variation affects their functional diversity and beta diversity has implications for their conservation and maintaining the ecosystem functions they provide. We determined how changing growth stages within sugarcane fields may influence the structure of bird communities. Our objectives were threefold. First, we compared species richness and diversity of birds in sugarcane fields to native savanna, which was cleared to make way for these plantations. We predicted that species richness and diversity would be higher in native

Table 1. Geographic position of the 12 study sites selected in savanna and in sugarcane plantations in north-eastern Eswatini. The latitude and longitude (both in decimal degrees) refer to the midpoint of each site. Also shown is the size of each sugarcane field (in hectares).

Land-use	Sites	Latitude	Longitude	Sugarcane field size (ha)
Savanna	N1	-26.1412	32.0072	-
Savanna	N2	-26.1436	31.9977	-
Savanna	N3	-26.1558	31.9966	-
Sugarcane	S1	-26.1594	31.9643	5.5
Sugarcane	S2	-26.1467	31.9637	14.9
Sugarcane	S3	-26.1560	31.9586	9.8
Sugarcane	S4	-26.1224	31.9442	10.6
Sugarcane	S5	-26.1078	31.9336	31.2
Sugarcane	S6	-26.1199	31.9499	22.9
Sugarcane	S7	-26.1974	31.9605	14.8
Sugarcane	S8	-26.1988	31.9703	18.3
Sugarcane	S9	-26.2146	31.9644	22.4

savanna compared with sugarcane. Second, we compared the species composition of birds in sugarcane fields of different growth stages, with each other and with native savanna. We predicted that bird communities would change as the sugarcane in the fields grew to maturation, with the tallest fields having their composition most closely resembling that of neighboring savanna communities. Third, we compared taxonomic and functional beta diversity of bird communities in sugarcane fields with those in native savanna. We predicted that functional beta diversity would be higher in sugarcane fields compared with native savanna because of the extensive changes in habitat structure in the fields (the different growth stages), allowing birds with different traits to inhabit the same field at different stages of crop maturation. We also predicted that taxonomic beta diversity over time would be higher in sugarcane fields as a result of increased turnover as species associated with bare ground give way to those associated with short grasslands (short sugarcane), and then with shrub habitats (medium and tall sugarcane).

2. Methods

2.1. Materials and methods

2.1.1. Study area

Our study was conducted in the Lowveld physiographic region of Eswatini, a low-lying region situated between the northern Drakensberg Escarpment in the west and the Lubombo Mountain range to the east; the Lowveld is the warmest and the driest region in the country (Figure 1). The region experiences hot, wet summers and cool, dry winters with mean daily temperatures of 26 °C and 18 °C, respectively. This area receives a mean annual rainfall of 574 mm and about 80% of the rain is

received during the wet season. The study area encompassed three large sugarcane estates (Simunye, Mhlume and Tambankulu) covering over 20,000 ha (Terry and Ogg, 2017) adjacent to three protected areas (Hlane Royal National Park, Mlawula Nature Reserve and Mbuluzi Game Reserve) that have a heterogeneous landscape of native savanna vegetation (McCleery et al., 2018; Monadjem, 2005). The growing cycle of sugarcane in Eswatini is roughly ten months from planting to harvest. The size of each field varies between 5 and 32 ha (Table 1), in which sugarcane is planted once and allowed to sprout after harvest for a number of years before replanting. Because different fields are planted at different times, together they represent a mosaic of different sugarcane growth stages at any one time. This provided us with a unique study design to determine the response of birds to these different growth stages, independent of season.

2.1.2. Study design

We conducted the study in two land-uses: commercial sugarcane plantations (hereafter sugarcane) and native savanna (hereafter savanna). We randomly selected nine sites within sugarcane, and three sites in neighbouring savanna (Mbuluzi Game Reserve) to serve as controls to reflect reference native vegetation that was cleared for sugarcane. Our sampling sites were situated between 26° 6' 32" and 26° 11' 55"S, and 32° 0' 26" and 31° 59' 51"E (Table 1). Sites were 1–10 km apart from each other, and those in sugarcane were at least 500 m away from any patches of native habitat. To capture the different stages of growth, we classified sugarcane fields into four categories in each survey session: emerging (fields that were either bare or had recently sprouted plants; sugarcane was 0–0.29 m tall), short (0.30–0.99 m), medium (1.00–1.99 m) and tall (>2.00 m). Sugarcane height was measured (to the nearest

Table 2. The total number of transects conducted in each sugarcane growth stage (emerging, short, medium, and tall) and savanna during the 10 sampling sessions in north-eastern Eswatini. Also included are the dates for the period on which surveys were conducted.

Session	Date	Emerging	Short	Medium	Tall	Savanna
1st	12 Jun – 6 Jul 2017	8	4	0	24	12
2nd	30 Jul – 6 Aug 2017	4	8	0	24	12
3rd	4 Sep – 11 Sep 2017	4	4	8	20	12
4th	10 Oct – 17 Oct 2017	4	8	12	12	12
5th	14 Nov – 21 Nov 2017	12	8	12	4	12
6th	16 Dec – 23 Dec 2017	0	8	16	12	12
7th	24 Jan – 1 Feb 2018	0	0	4	32	12
8th	27 Feb – 6 Mar 2018	0	0	0	36	12
9th	15 Apr – 22 Apr 2018	4	0	0	32	12
10th	11 May – 19 May 2018	12	0	0	24	12
Total		48	40	52	220	240

Table 3. Total number of transects conducted in each sugarcane growth stage (emerging, short, medium, and tall) and savanna during each season at each of the 12 sites in north-eastern Eswatini. Numbers in parentheses represent the total number of transects conducted in the dry and wet season, respectively.

Site	Emerging	Short	Medium	Tall	Savanna	Total
N1	-	-	-	-	40 (20, 20)	40 (20, 20)
N2	-	-	-	-	40 (20, 20)	40 (20, 20)
N3	-	-	-	-	40 (20, 20)	40 (20, 20)
S1	4 (4, 0)	8 (8, 0)	8 (8, 0)	16 (0, 16)	-	40 (20, 20)
S2	4 (0, 4)	4 (0, 4)	0 (0, 0)	32 (20, 12)	-	40 (20, 20)
S3	4 (4, 0)	4 (0, 4)	4 (0, 4)	16 (16, 12)	-	40 (20, 20)
S4	12 (12, 0)	4 (4, 0)	8 (4, 4)	16 (0, 16)	-	40 (20, 20)
S5	0 (0, 0)	8 (4, 4)	4 (0, 4)	28 (16, 12)	-	40 (20, 20)
S6	4 (4, 0)	4 (4, 0)	8 (0, 8)	24 (12, 12)	-	40 (20, 20)
S7	12 (8, 4)	4 (4, 0)	8 (8, 0)	16 (0, 16)	-	40 (20, 20)
S8	4 (0, 4)	4 (0, 4)	4 (0, 4)	28 (20, 8)	-	40 (20, 20)
S9	4 (0, 4)	0 (0, 0)	4 (0, 4)	32 (20, 12)	-	40 (20, 20)

0.1 m) once in every session by using a 5 m ruler. We repeatedly surveyed birds and sampled vegetation on one 200 m transect per site ($n = 12$, Tables 2 and 3).

2.1.3. Bird counts

We commenced bird counts in June 2017 and repeated them every 5th week through to May 2018 resulting in 10 sampling sessions that covered both wet (November to April) and dry (May to October) seasons (Table 2). Each season comprised of five sampling sessions. During each session, we conducted counts along line transects for four consecutive mornings. All bird counts were conducted by the same observer (SML) following standard procedures outlined in Bibby et al. (2000). We randomized the sequence in which sites were visited. Before commencing a transect, we waited 1 min to allow the birds to settle, after which, we walked at a constant pace recording every bird heard and seen within 100 m on either side, a process that took about 15 min per transect. Following McCleery et al. (2018), we did not record birds flying overhead unless they were specifically using that land-use for foraging (such as swifts and swallows foraging repeatedly over the same area, as opposed to birds flying above the site that were clearly transiting from one area to another). All bird counts were conducted in the morning between sunrise and five hours thereafter. Bird surveys were not conducted under rainy or windy weather conditions (Bibby et al., 2000).

2.1.4. Species richness and diversity

To determine how completely we had surveyed our sites, we created species-accumulation curves for the sugarcane (and separate curves for each growth stage) and savanna sites using the function 'specaccum' in the R package vegan (Oksanen et al., 2016). To understand the response of birds to change in sugarcane height we calculated species richness per transect across all sessions as the sum of species recorded. We also used estimated species richness across all sessions using the Chao species richness estimator in the vegan function 'estimateR', which adjusts observed species richness based on the number of 'singletons' and 'doubletons' in the data (assuming that when these are common, many species may have been gone undetected). We calculated species diversity as the Shannon-Wiener (Shannon) diversity index (H') and Simpson diversity index (D) in vegan by using the mean abundances for each species.

To evaluate differences in observed species richness and diversity in the different sugarcane and savanna sites, we fitted generalized linear mixed models (GLMMs) in the lme4 package, function 'glmer' for species richness and 'lmer' for Shannon diversity (Bates et al., 2015). We fitted a Poisson log link function for species richness and Gaussian identity link function for species diversity. Site was included as a random effect. Habitat (the four growth stages of sugarcane and the savanna) and season (dry and wet) were included as explanatory variables, as was the interaction between habitat and season. The Akaike Information Criterion

(AICc) value was used to compare models, with the best model chosen based on the lowest AICc value while those with $\Delta AICc < 2$ were considered to be competing models (Burnham and Anderson, 2004; Johnson and Omland, 2004). All analyses were conducted in R version 3.3.4 (R Core Team, 2018).

2.1.5. Community composition

To assess differences in bird assemblages in the sugarcane growth stages we compared bird community composition in the different habitats by using species abundance data to perform a non-metric multidimensional scaling (NMDS) ordination using the Bray-Curtis distance measure. We used the function 'metaMDS' in the vegan package (Oksanen et al., 2016). We computed 'stress', a parameter that measures the representation efficiency of the obtained dimensions, with stress values < 0.1 showing good separation and stress > 0.2 representing poor separation in the data. We then performed an Analysis of Similarities (ANOSIM) to test the significance of variation observed in the bird communities in different habitats. All analysis were done in R version 3.3.4 (R Core Team, 2018).

2.1.6. Taxonomic beta diversity

To determine the influence of spatial and temporal variability of sugarcane plantations we computed taxonomic beta diversity metrics by the dissimilarity in species composition using presence/absence species data. We partitioned total beta diversity (Sørensen dissimilarity index β_{sor}) into contributions by species turnover (Simpson's dissimilarity: β_{sim}), and nestedness-resultant dissimilarity (β_{nes}), following Baselga (2012; 2010). We calculated total beta diversity in two separate ways: a) between sites (spatial beta diversity); and b) within each site over time (temporal beta diversity) both analyses were pooled by seasons (dry and wet). β_{sor} was measured as Sørensen derived dissimilarity, which accounts for the total variation between assemblages, β_{sim} was measured as a Simpson derived dissimilarity which accounts for the substitution of species in a site over time, and β_{nes} (difference between β_{sor} and β_{sim}) was measured as nestedness-resultant fraction of Sørensen derived dissimilarity which accounts for the loss or gain of species in a habitat. Each of these indices varies between 0 and 1, with lower values indicating a greater proportion of shared species richness, and larger values indicating greater dissimilarity between sites. The calculations were done using the function 'beta.pair.abund' in the package betapart (Baselga and Orme, 2012). We used t-tests or Mann-Whitney tests to compare levels of species turnover and loss in the two land-uses depending on the distribution of the data.

2.1.7. Functional beta diversity and functional redundancy

To quantify changes in species trait composition among sites and over time, we estimated functional beta diversity by selecting traits of birds that included: wing, beak, and tarsus length, and body mass since these

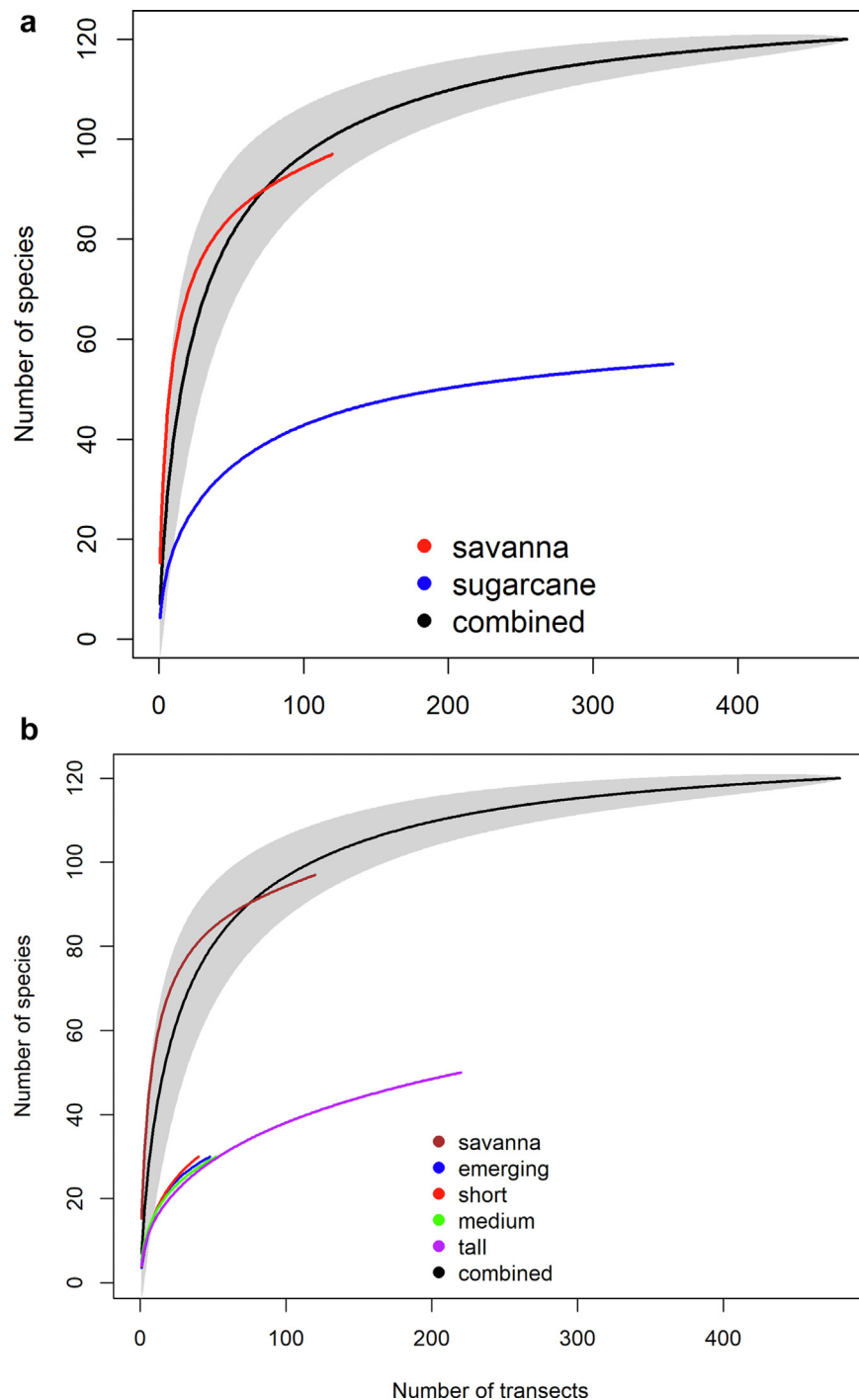


Figure 2. Species accumulation curves for: (a) birds surveyed in the savanna (red curve) and sugarcane (blue curve). The black curve represents all birds (i.e. both savanna and the sugarcane); (b) birds surveyed in the four growth stages: emerging (blue curve), short (red curve), medium (green curve), and tall (purple curve) sugarcane, and native savanna (brown curve) habitats in north-eastern Eswatini.

traits are associated with the functional role of a species (Coetsee and Chown, 2016). Species trait data were extracted from Hockey et al. (2005). Following the methods proposed by Baselga (2010; 2013), we first performed a principal component analysis (PCA) on the species traits to create four PCA axes. We used the species presence-absence data together with the PCA axes to compute functional beta diversity. The calculations were done using the function `'function.beta.pair'` in the package `betapart` (Baselga and Orme, 2012). We conducted a Kruskal-Wallis test to test for differences in functional beta diversity

between the two land-uses (savanna and sugarcane). We then used Dunn's multiple comparison test if the null hypothesis was rejected.

Lastly, we used species abundance data and traits data to calculate two measures of functional redundancy: functional alpha diversity (Rao's index Q ; which integrates the abundances and a measure of taxonomic distance between species by using species functional traits) and functional uniqueness (U) using the `'uniqueness'` function in Ricotta et al. (2016). Functional uniqueness is summarized as the ratio between Rao index Q and the Simpson index which considers all species as equally and

Table 4. A list of the bird species recorded in the savanna and sugarcane growth stages in north-eastern Eswatini. The different sugarcane growth stages are represented by emerging, short, medium, and tall. The numbers represent the number of individuals per sugarcane growth stage and savanna recorded across all sessions. The asterisks (*) represent ground foraging bird. Species are ordered alphabetically by scientific name.

Scientific name	English name	Emerging	Short	Medium	Tall	Savanna
<i>Acrocephalus baeticatus</i>	African Reed-Warbler	11	0	17	373	0
<i>Alopothen aegyptiaca</i>	Egyptian Goose	0	0	0	0	1
<i>Andropadus importunus</i>	Sombre Greenbul	0	0	0	0	28
<i>Anthus cinnamomeus</i>	African Pipit*	156	37	38	14	0
<i>Apalis flavida</i>	Yellow-breasted Apalis	0	0	0	0	26
<i>Apus caffer</i>	White-rumped Swift	0	4	0	1	0
<i>Ardea melanocephala</i>	Black-headed Heron	2	0	1	4	2
<i>Batis molitor</i>	Chin-spot Batis	0	0	0	0	102
<i>Bostrychia hagedash</i>	Hadedda Ibis	0	0	0	19	3
<i>Bradypterus baboecala</i>	Little Rush-Warbler	0	0	22	266	0
<i>Bubulcus ibis</i>	Cattle Egret*	80	1	0	8	0
<i>Buphagus erythrorhynchus</i>	Red-billed Oxpecker	0	0	0	0	60
<i>Burhinus capensis</i>	Spotted Thick-knee	9	0	0	0	0
<i>Buteo vulpinus</i>	Steppe Buzzard	0	2	2	2	2
<i>Bycanistes bucinator</i>	Trumpeter Hornbill	0	0	0	0	5
<i>Camaroptera brachyura</i>	Green-backed Camaroptera	0	0	0	0	28
<i>Campephaga flava</i>	Black Cuckooshrike	0	0	0	0	10
<i>Campepthera abingoni</i>	Golden-tailed Woodpecker	0	0	0	0	27
<i>Cecropis abyssinica</i>	Lesser Striped Swallow	8	8	4	14	0
<i>Cecropis semirufa</i>	Red-breasted Swallow	0	0	6	0	0
<i>Centropus burchellii</i>	Burchell's Coucal	2	0	0	13	17
<i>Cercotrichas leucophrys</i>	White-browed Scrub-Robin	0	0	0	0	110
<i>Chalcomitra amethystina</i>	Amethyst Sunbird	0	0	0	0	6
<i>Chalcomitra senegalensis</i>	Scarlet-chested Sunbird	0	0	0	0	29
<i>Charadrius pecuarius</i>	Kittlitz's Plover	13	0	0	0	0
<i>Charadrius tricollaris</i>	Three-banded Plover	0	1	0	0	0
<i>Chrysococcyx caprius</i>	Diderick Cuckoo	0	0	0	0	3
<i>Chrysococcyx klaas</i>	Klaas's Cuckoo	0	0	0	0	1
<i>Ciconia episcopus</i>	Woolly-necked Stork*	5	1	0	2	0
<i>Cinnyricinclus leucogaster</i>	Violet-backed Starling	0	0	0	0	5
<i>Cinnyris mariquensis</i>	Marico Sunbird	0	0	0	0	4
<i>Cinnyris talatala</i>	White-bellied Sunbird	0	0	0	0	59
<i>Cisticola chiniana</i>	Rattling Cisticola	0	0	0	10	202
<i>Cisticola erythrops</i>	Red-faced Cisticola	0	0	0	1	0
<i>Cisticola juncidis</i>	Zitting Cisticola	0	13	93	104	0
<i>Cisticola natalensis</i>	Croaking Cisticola	0	0	0	1	1
<i>Clamator jacobinus</i>	Jacobin Cuckoo	0	0	0	0	2
<i>Colius striatus</i>	Speckled Mousebird	0	0	0	0	18
<i>Corvus albus</i>	Pied Crow	1	0	1	5	0
<i>Cossypha heuglini</i>	White-browed Robin-Chat	0	0	0	1	0
<i>Coturnix delegorguei</i>	Harlequin Quail	14	0	5	19	9
<i>Crithagra gularis</i>	Streaky-headed Seedeater	0	0	0	0	1
<i>Crithagra mozambicus</i>	Yellow-fronted Canary	8	3	18	78	192
<i>Cuculus clamosus</i>	Black Cuckoo	0	0	0	0	1
<i>Cuculus solitarius</i>	Red-chested Cuckoo	0	0	0	0	12
<i>Cypsiurus parvus</i>	African Palm-Swift	3	7	7	8	2
<i>Dendropicus fuscescens</i>	Cardinal Woodpecker	0	0	0	0	23
<i>Dendropicus namaquus</i>	Bearded Woodpecker	0	0	0	0	15
<i>Dicrurus adsimilis</i>	Fork-tailed Drongo	1	5	0	2	75
<i>Dryoscopus cubla</i>	Black-backed Puffback	0	0	0	0	52
<i>Elanus axillaris</i>	Black-shouldered Kite	0	0	3	3	0
<i>Emberiza flaviventris</i>	Golden-breasted Bunting	0	0	0	0	71
<i>Estrilda astrild</i>	Common Waxbill	2	1	164	286	25
<i>Euplectes albonotatus</i>	White-winged Widowbird	0	0	6	10	11
<i>Euplectes ardens</i>	Red-collared Widowbird	0	0	2	20	9
<i>Euplectes axillaris</i>	Fan-tailed Widowbird	20	24	207	390	28
<i>Euplectes orix</i>	Southern Red Bishop	0	0	26	44	0

(continued on next page)

Table 4 (continued)

Scientific name	English name	Emerging	Short	Medium	Tall	Savanna
<i>Falco subbuteo</i>	Eurasian Hobby	0	0	0	0	6
<i>Gallirex porphyreolophus</i>	Purple-crested Turaco	0	0	0	0	31
<i>Glareola pratincola</i>	Collared Pratincole	0	3	1	0	0
<i>Halcyon albiventris</i>	Brown-hooded Kingfisher	0	0	0	0	28
<i>Halcyon chelicuti</i>	Striped Kingfisher	0	0	0	0	23
<i>Halcyon senegalensis</i>	Woodland Kingfisher	0	0	0	0	15
<i>Haliaeetus vocifer</i>	African Fish-Eagle	0	0	0	0	6
<i>Hirundo albigularis</i>	White-throated Swallow	11	13	63	11	0
<i>Hirundo rustica</i>	Barn Swallow	25	5	63	282	10
<i>Hirundo smithii</i>	Wire-tailed Swallow	0	2	0	9	0
<i>Indicator indicator</i>	Greater Honeyguide	0	0	0	0	1
<i>Lagonosticta rubricata</i>	African Firefinch	0	0	0	0	33
<i>Lamprotornis nitens</i>	Cape Glossy Starling	0	1	0	5	20
<i>Laniarius ferrugineus</i>	Southern Boubou	0	0	0	1	5
<i>Lanius collurio</i>	Red-backed Shrike	0	0	0	1	14
<i>Leptoptilos crumeniferus</i>	Marabou Stork	1	0	0	0	0
<i>Lissotis melanogaster</i>	Black-bellied Bustard	0	0	1	0	9
<i>Lybius torquatus</i>	Black-collared Barbet	0	0	0	0	57
<i>Macronyx croceus</i>	Yellow-throated Longclaw	0	0	0	0	13
<i>Malaconotus blanchoti</i>	Grey-headed Bush-Shrike	0	0	0	0	46
<i>Melaenornis pammelaina</i>	Southern Black Flycatcher	0	0	0	1	34
<i>Merops apiaster</i>	European Bee-eater	0	0	0	2	56
<i>Merops bullockoides</i>	White-fronted Bee-eater	0	0	0	0	2
<i>Merops pusillus</i>	Little Bee-eater	0	0	0	0	7
<i>Milvus migrans</i>	Black Kite	1	1	1	1	1
<i>Motacilla aguimp</i>	African Pied Wagtail	0	0	0	3	2
<i>Muscicapa caerulescens</i>	Ashy Flycatcher	0	0	0	0	6
<i>Muscicapa striata</i>	Spotted Flycatcher	0	0	0	0	1
<i>Nicator gularis</i>	Eastern Nicator	0	0	0	0	14
<i>Nilaus afer</i>	Brubru	0	0	0	0	38
<i>Numida meleagris</i>	Helmeted Guineafowl*	120	46	15	0	22
<i>Oena capensis</i>	Namaqua Dove	0	0	0	1	0
<i>Oriolus larvatus</i>	Black-headed Oriole	0	0	0	0	33
<i>Parus niger</i>	Southern Black Tit	0	0	0	0	26
<i>Passer diffusus</i>	Southern Grey-headed Sparrow	0	0	0	0	8
<i>Petronia superciliaris</i>	Yellow-throated Petronia	0	0	0	0	49
<i>Phoeniculus purpureus</i>	Green Wood-Hoopoe	0	0	0	0	14
<i>Phylloscopus trochilus</i>	Willow Warbler	0	0	0	0	4
<i>Ploceus ocularis</i>	Spectacled Weaver	1	0	0	1	2
<i>Polyboroides typus</i>	African Harrier-Hawk	0	3	1	1	0
<i>Prinia subflava</i>	Tawny-flanked Prinia	8	8	43	99	94
<i>Prionops plumatus</i>	White-crested Helmet-Shrike	0	0	0	0	17
<i>Pternistis natalensis</i>	Natal Spurfowl	0	0	0	0	7
<i>Pternistis swainsonii</i>	Swainson's Spurfowl	0	0	0	0	2
<i>Pycnonotus tricolor</i>	Dark-capped Bulbul	2	0	1	72	262
<i>Quelea quelea</i>	Red-billed Quelea	0	0	0	0	132
<i>Rhinopomastus cyanomelas</i>	Common Scimitarbill	0	0	0	0	30
<i>Saxicola torquatus</i>	African Stonechat	4	1	0	55	0
<i>Scopus umbretta</i>	Hamerkop	0	1	0	0	1
<i>Spermestes cucullatus</i>	Bronze Mannikin	0	0	2	11	8
<i>Streptopelia capicola</i>	Cape Turtle-Dove	2	2	2	0	106
<i>Streptopelia semitorquata</i>	Red-eyed Dove	0	1	0	5	29
<i>Streptopelia senegalensis</i>	Laughing Dove	0	0	0	5	12
<i>Sylvietta rufescens</i>	Long-billed Crombec	0	0	0	0	33
<i>Tchagra australis</i>	Brown-crowned Tchagra	0	0	0	0	23
<i>Tchagra senegalus</i>	Black-crowned Tchagra	0	0	0	0	74
<i>Telophorus sulfureopectus</i>	Orange-breasted Bush-Shrike	0	0	0	0	33
<i>Terathopus ecaudatus</i>	Bateleur	0	0	0	0	1
<i>Terpsiphone viridis</i>	African Paradise-Flycatcher	0	0	0	0	11

(continued on next page)

Table 4 (continued)

Scientific name	English name	Emerging	Short	Medium	Tall	Savanna
<i>Tockus alboterminatus</i>	Crowned Hornbill	0	0	0	0	2
<i>Trachyphonus vaillantii</i>	Crested Barbet	0	0	0	0	21
<i>Treron calvus</i>	African Green-Pigeon	0	0	0	0	4
<i>Turdoides jardineii</i>	Arrow-marked Babbler	0	0	0	4	39
<i>Turdus libonyanus</i>	Kurrichane Thrush	0	0	0	0	29
<i>Turnix sylvaticus</i>	Kurrichane Buttonquail	0	1	8	24	8
<i>Turtur chalcospilos</i>	Emerald-spotted Wood-Dove	0	0	0	2	77
<i>Upupa africana</i>	African Hoopoe	0	0	0	0	7
<i>Uraeginthus angolensis</i>	Blue Waxbill	0	0	0	1	55
<i>Urocolius indicus</i>	Red-faced Mousebird	0	0	0	0	131
<i>Vanellus coronatus</i>	Crowned Lapwing*	61	5	0	2	0
<i>Vanellus senegallus</i>	African Wattled Lapwing*	68	17	3	0	1
<i>Vidua chalybeata</i>	Village Indigobird	0	0	0	0	1
<i>Vidua macroura</i>	Pin-tailed Whydah	0	1	6	4	0

maximally dissimilar (Ricotta et al., 2016; Ricotta and Marignani, 2007). We used a t-test to determine if functional alpha diversity and functional uniqueness differed between the two land-uses.

3. Results

3.1. Species richness and diversity

We recorded a total of 7,350 detections of birds belonging to 124 species and 58 families. Of these, 103 species from 52 families were recorded in savanna compared with 55 species from 31 families in sugarcane. The species accumulation curve for sugarcane (overall) was approaching the asymptote whereas that for savanna was still rising, although the rate of increase appeared to be decreasing and had passed the inflection point (Figure 2a). The species accumulation curves for each sugarcane growth stage did not appear to have reached an asymptote suggesting that the entire community was not detected (Figure 2b). The emerging fields were dominated by ground bird species which included lapwings and other species of plovers (Charadriidae), guineafowls (Numididae), and pipits (Motacillidae), which were almost entirely absent in native savanna (Table 4). Bird species richness per transect was 3–5 species in sugarcane and 13–19 species in savanna (Figure 3a, Figure 3c and Figure 4a), a three- to five-fold difference. The Chao estimated species richness was higher than the recorded species richness, however, the two measures showed the same trend (Figure 3e). Overall, species richness increased with sugarcane growth (from emerging to medium) and then decreased again in the tall sugarcane, yielding a slightly hump-shaped curve (Figure 3a and Figure 3c). Our results suggested that variation in species richness was best explained by a model that included an interaction between habitat and season (AICc = 2067.1) (Table 5). Based on this model, species richness in emerging and tall sugarcane growth stages were lower than that in the other growth stages, and highest in savanna, and species richness was higher in the wet season than the dry season, with a marginally significant interaction between the short growth stage and season (Figure 3a, Table 6).

A similar pattern was observed for bird species diversity with H' = 0.9–1.5 per transect in sugarcane and 2.0–3.0 per transect in savanna (Figure 3b, Figure 3d and Figure 4b), a difference of about twofold. The Simpson diversity index also showed the same trend (Figure 4c). As observed with species richness, species diversity (Shannon diversity) also increased with the growth of sugarcane and then decreased again in the tall sugarcane (Figure 3b and Figure 3d). The GLMM showed that the Shannon diversity index was best explained by a model that included an interaction between habitat and season (AICc = 501.3) (Table 5). Based on this model, species diversity was lower in emerging and tall sugarcane than in the other growth stages and highest in the savanna; furthermore, species diversity was higher in the wet season than the dry season and

there was a significant interaction between the wet season and short sugarcane (Table 6).

3.2. Community composition

The NMDS ordination had a stress value of 0.15 and hence conveyed a good representation of the data. Bird species composition differed significantly between the various growth stages of sugarcane and savanna (ANOSIM, $R = 0.603$, $p < 0.001$). Bird species composition in savanna was distinct from that in sugarcane, irrespective of growth stage (Figure 5). Within sugarcane fields, species composition exhibited significant overlap between growth stages, but emerging and short fields were mostly separated from medium and tall fields (Figure 5).

3.3. Taxonomic beta diversity

Taxonomic (spatial) beta diversity, as measured by changes in species composition between sites, was low when comparing sites within savanna or within sugarcane but was high when comparing sites in savanna with those in sugarcane (Figure 6a). The turnover component of beta diversity accounted for most of its variation (Figure 6c), with nestedness values being much lower (Figure 6e). Taxonomic (temporal) beta diversity, as measured by changes in species composition at the same site over time, was higher in sugarcane than in savanna (Figure 7a, $W = 12153$, $p < 0.001$).

3.4. Functional beta diversity

There was a tendency for functional beta diversity to be highest between savanna and sugarcane sites, but this was masked by significant variation within sugarcane sites (Figure 6b). There was significant variation in functional beta diversity between sites; these values were consistently low in savanna sites but varied greatly in sugarcane sites (Figure 6b). In contrast to the pattern observed for taxonomic beta diversity, the turnover component of functional beta diversity did not account for most of its variation, with nestedness values being similar to those of turnover (Figure 6d and Figure 6f). This can also be seen by the comparison of functional beta diversity between habitats, which was low within savanna sites, but high between savanna and sugarcane, as well as within sugarcane ($H = 9.128$, $df = 2$, $P = 0.010$) (Figure 7b). The Dunn's multiple comparison test showed that functional beta diversity only differed significantly when we compared results for sites within savanna with those between savanna and sugarcane ($p = 0.018$). However, none of the other comparisons were significant (Table 7).

Functional alpha diversity (as measured by Rao's index Q) was higher in sugarcane than in savanna (Figure 7c). There was little variation in this index in savanna sites; in contrast, this index varied greatly in sugarcane

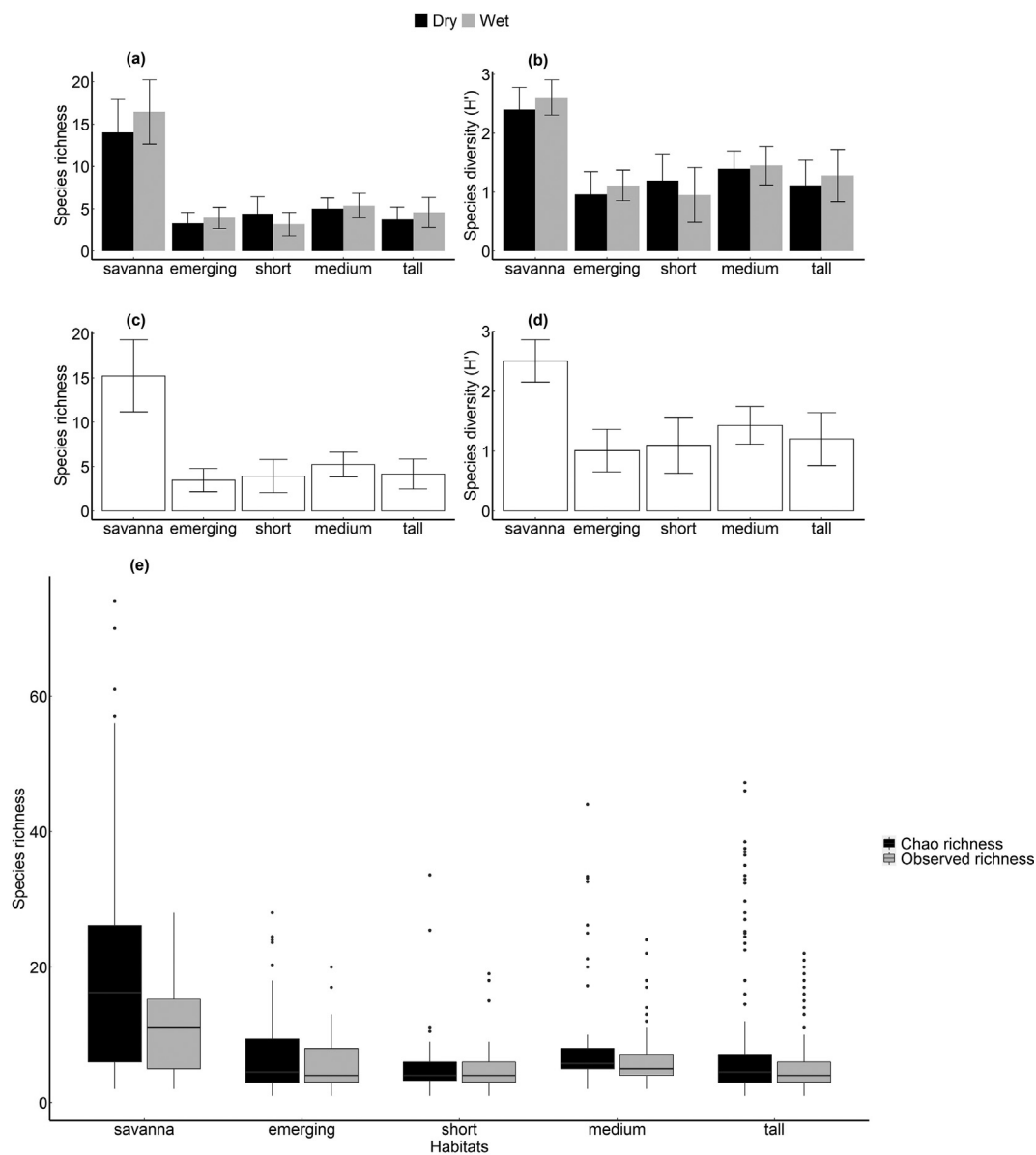


Figure 3. Mean number of: (a) species; and (b) Shannon diversity index recorded per transect in the two land-uses in the dry and wet season. Mean number of: (c) species; and (d) Shannon diversity recorded per habitat across all sessions. Error bars represent standard error. Boxplot showing: (e) a comparison of the observed bird species richness and estimated species richness (Chao estimator) for the savanna and sugarcane sites, with “emerging”, “short”, “medium”, and “tall” represent the different growth stages in the sugarcane.

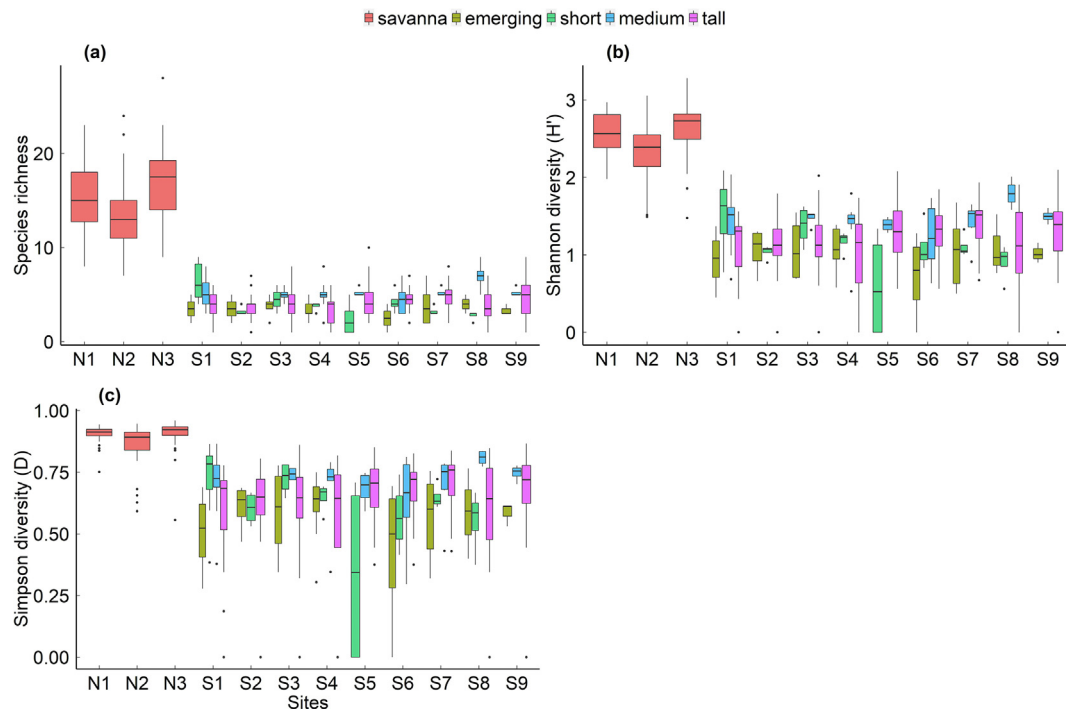


Figure 4. Diversity metrics per site in sugarcane and savanna showing: (a) species richness; (b) Shannon diversity; and (c) Simpson diversity. N1–N3 represent the three sites in savanna and S1–S9 represent the nine different sites in the sugarcane. The different colors represent the different habitats: savanna, emerging, short, medium, and tall (see text for definitions).

sites. Furthermore, this index differed significantly between the two land-uses ($t = 4.053$, $df = 9.621$, $p = 0.003$). The functional uniqueness index (U) was higher in sugarcane than in savanna ($t = 4.560$, $df = 9.561$, $p = 0.001$) (Figure 7d).

4. Discussion

We examined bird communities in sugarcane fields of different growth stages and compared these with the communities in neighbouring native savanna. We recorded more bird species in the savanna than in any of the growth stages of sugarcane. However, despite the presumed homogeneity of monocultures, our study demonstrated that the different growth stages of sugarcane created spatial and temporal variability, thus allowing distinctly different bird communities to persist in this agricultural landscape. This is the first study to show such heterogeneity in avian communities in a monoculture crop (due to variation in growth stages), although such a pattern has previously been reported in North American grasslands that were burned in patches, creating a similar mosaic to that seen in Eswatini sugarcane plantations (Coppedge et al., 2008; Farneda

et al., 2019). It is also worth mentioning that the pattern shown by our results may also be applicable to other monoculture crops that have significant structural variation in growth stages. However, to the best of our knowledge, such studies looking at the influence of different growth stages of crops on avian diversity have not been conducted in other cropping systems.

The fact that sugarcane changes drastically in structure over the growing season may explain the higher taxonomic beta diversity and functional uniqueness here compared with native savanna, which changes less in the same space of time. This pattern appears largely driven by the fact that bare fields (i.e. those that had recently been planted) harboured birds associated with open-ground, such as species belonging to the families Motacillidae, Numididae, and Charadriidae (Hockey et al., 2005), which are a good predictor for grassland species (Fisher and Davis, 2010). This implies that sugarcane agro-ecosystems provide an important habitat for ground foraging bird species, which is currently limited in neighbouring savanna landscapes, perhaps as a result of bush encroachment (Monadjem, 2005; Sirami and Monadjem, 2012). This may also extend to ground-nesting species (Narwade et al., 2010)

Table 5. The generalised linear mixed models used to test the response of species richness and diversity to the fixed effects of habitat (i.e. growth stages of sugarcane fields and native savanna) and season. Also reported are the number of parameters (K), the cumulative corrected Akaike's Information Criteria ($AICc$), differences in $AICc$ of models compared to the top model ($\Delta AICc$), model weights ($AICcWt$), and the -2 log-likelihood yield for each model ($Res.LL$).

Model	K	AICc	Delta_AICc	AICcWt	Cum.Wt	Res.LL
Species richness						
Season × habitat	11	2067.1	0.000	0.999	0.999	-1022.3
Habitat	6	2080.3	13.2	0.001	1.00	-1034.1
Season	3	2115.7	48.4	0.000	1.00	-1054.8
Null	2	2132.2	65.1	0.000	1.00	-1064.1
Shannon diversity						
Season × habitat	12	501.3	0.00	0.984	0.984	-238.3
Habitat	7	509.6	8.25	0.016	1.000	-247.7
Season	4	563.0	61.6	0.000	1.000	-277.4
Null	3	574.0	72.7	0.000	1.000	-284.0

Table 6. The top models, based on generalised linear mixed models (see Table 5), explaining species richness and diversity by habitat (the four different sugarcane growth stages and native savanna) and season (wet and dry). Also, shown are parameter estimates (β), standard errors (SE), p-values, and confidence intervals; None of the parameters overlap zero and therefore all are significant.

	β	SE	z value	Pr (> z)	Confidence intervals	
					2.50%	97.50%
Species richness						
Intercept (sugarcane-emerging, season – dry)	1.204	0.102	11.8	<2e-16	0.999	1.400
Season-wet	0.157	0.163	0.964	0.335	-0.167	0.473
Sugarcane -medium	0.404	0.141	0.862	0.004	0.127	0.682
Savanna	1.433	0.114	12.5	<2e-16	1.209	1.661
Sugarcane- short	0.282	0.139	2.028	0.043	0.009	0.555
Sugarcane-tall	0.125	0.114	1.090	0.276	-0.097	0.354
Season-wet x sugarcane-medium	-0.088	0.208	-0.427	0.669	-0.491	0.321
Season-wet x savanna	0.002	0.170	0.012	0.991	-0.327	0.339
Season -wet x sugarcane - short	-0.483	0.235	-2.055	0.040	-0.947	-0.023
Season -wet x sugarcane-tall	0.025	0.179	0.141	0.888	-0.323	0.381
	β	SE	t value	Pr (> z)	Confidence intervals	
					2.50%	97.50%
Shannon diversity						
Intercept (sugarcane – emerging, season – dry)	0.986	0.074	13.3	<2e-16	0.840	1.134
Season-wet	0.104	0.124	0.837	0.403	-0.142	0.349
Sugarcane -medium	0.418	0.114	3.67	0.0002	0.194	0.641
Savanna	1.415	0.096	14.8	<2e-16	1.221	1.602
Sugarcane- short	0.137	0.084	2.00	0.046	0.004	0.427
Sugarcane-tall	0.104	0.124	1.63	0.105	-0.032	0.303
Season-wet x sugarcane-medium	-0.056	0.168	-0.332	0.740	-0.387	0.276
Season-wet x savanna	0.102	0.143	0.712	0.477	-0.181	0.385
Season -wet x sugarcane - short	-0.353	0.177	-1.994	0.047	-0.702	-0.005
Season -wet x sugarcane-tall	0.035	0.138	0.256	0.800	-0.181	0.385

but this requires further study. However, because habitat structure in sugarcane is transient, with short residence time of any one particular growth phase of the crop, these fields may end up being a sink habitat (Pulliam, 1988) or even worse, an ecological trap (Battin, 2004) that cannot support populations in the long-term; this requires further research attention. Additionally, our study provides evidence of high taxonomic (spatial) turnover when comparing sites in the savanna to those in sugarcane, while it was low when comparing sites within the sugarcane. This indicates the negative impact that sugarcane has on avian and other faunal assemblages (Rivera-Pedroza et al., 2019) because in general, sugarcane plantations are a homogenous environment with greatly reduced variation. Higher taxonomic temporal turnover was observed in sugarcane compared to savanna, which may be a result of the bird assemblage responding to rapid changes in the growth stages of sugarcane fields.

Our results demonstrate that bird species composition varied significantly in the different growth stages and savanna habitats as shown by the NMDS plot (Figure 5). The emerging and short sugarcane fields harboured ground dwelling species that included: *Anthus cinnamomeus*, *Numida meleagris*, *Bubulcus ibis*, *Vanellus coronatus*, and *Vanellus senegallus*. The composition of bird species changed with the height of the sugarcane and medium and tall sugarcane sites were dominated by small sized species that prefer densely vegetated areas and cover. These included *Bradypterus baboecala*, *Acrocephalus baeticatus*, *Estrilda astrild*, and *Cisticola juncidis* (Table 4). Furthermore, *Euplectes axillaris*, which was recorded in all the growth stages of the sugarcane, was an order of magnitude more abundant in the medium and tall sugarcane fields than in savanna (Table 4). Our study showed that a large proportion of the savanna species did not occur in sugarcane fields at all or only in tall fields (Table 4), and the few that were recorded in sugarcane were typically generalist species such as

the *Pycnonotus tricolor* (Monadjem, 2005; Sirami and Monadjem, 2012).

We also demonstrated that native savanna supported more species of birds at greater densities and with higher diversity, as well as with a significantly different community composition than sugarcane fields, regardless of their stage of growth. Species richness and diversity did not show a consistent pattern with sugarcane growth. These metrics showed a hump shaped response increasing from emerging to medium sugarcane but decreased from medium to tall sugarcane. We do not know the reason for this, but it may be because tall sugarcane represents an impenetrable thicket for most savanna-associated birds, that are typically found in more open habitats. The observed species richness, Chao species richness estimate and the two species diversity metrics (Shannon and Simpson) showed the same trend in both the savanna and the four sugarcane growth stages. Our species accumulation curves (Figure 2a) suggest that we had sufficiently sampled the sugarcane bird community, but not the savanna community, indicating that the differences in richness and diversity we observed are likely conservative and may be more extreme in reality. The low number of species observed in sugarcane is consistent with findings of other studies that have reported a reduction in species richness and diversity in farmlands compared with native vegetation (Atkinson et al., 2002; Donald et al., 2001; Norris, 2008). For example, in Eswatini, the occurrence of nearly all bird species was negatively associated with sugarcane plantations (Stanton et al., 2020). The lower diversity in sugarcane compared to savanna may be due to the fact that savanna has a greater variation in vegetation structure and offers a greater diversity of resources, such as nesting sites and shelter (Casas et al., 2016; Laube et al., 2008; Norfolk et al., 2017) that are lacking in sugarcane fields. Additionally, species richness and diversity were higher in the savanna during the wet than the dry season while seasonality did not have an influence on bird species richness and diversity in the

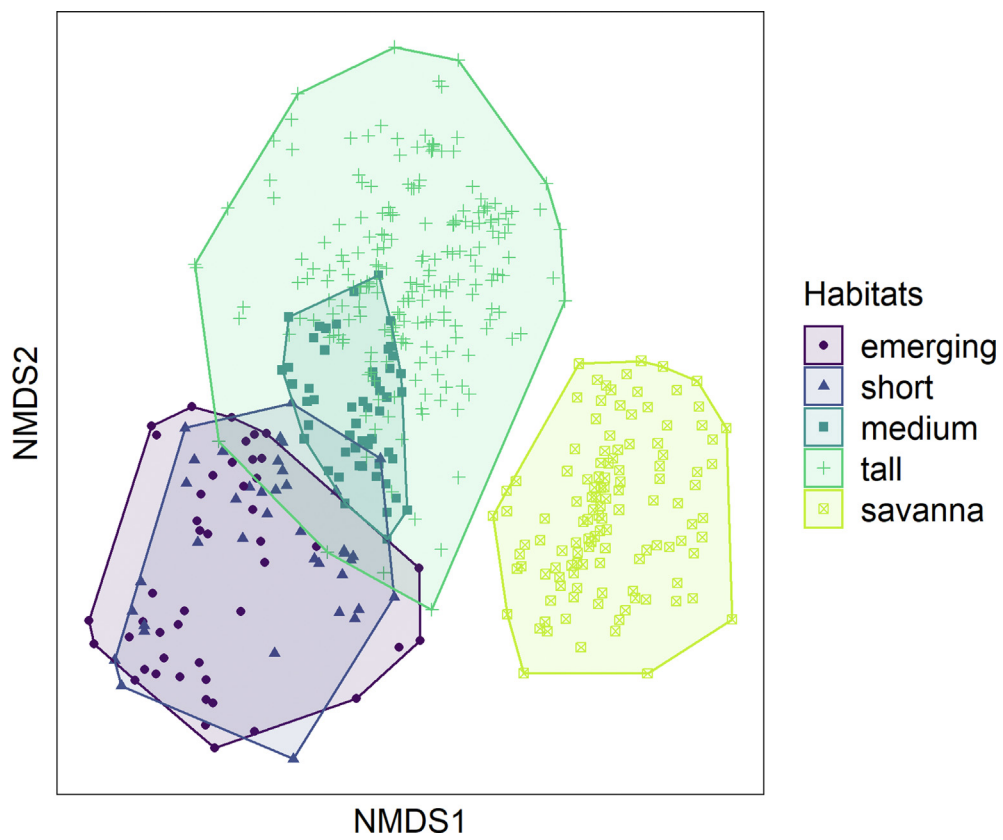


Figure 5. Non-metric multi-dimensional scaling ordination showing the composition of bird species in the different habitats as represented by sugarcane growth stages (emerging, short, medium and tall) and savanna in north-eastern Eswatini.

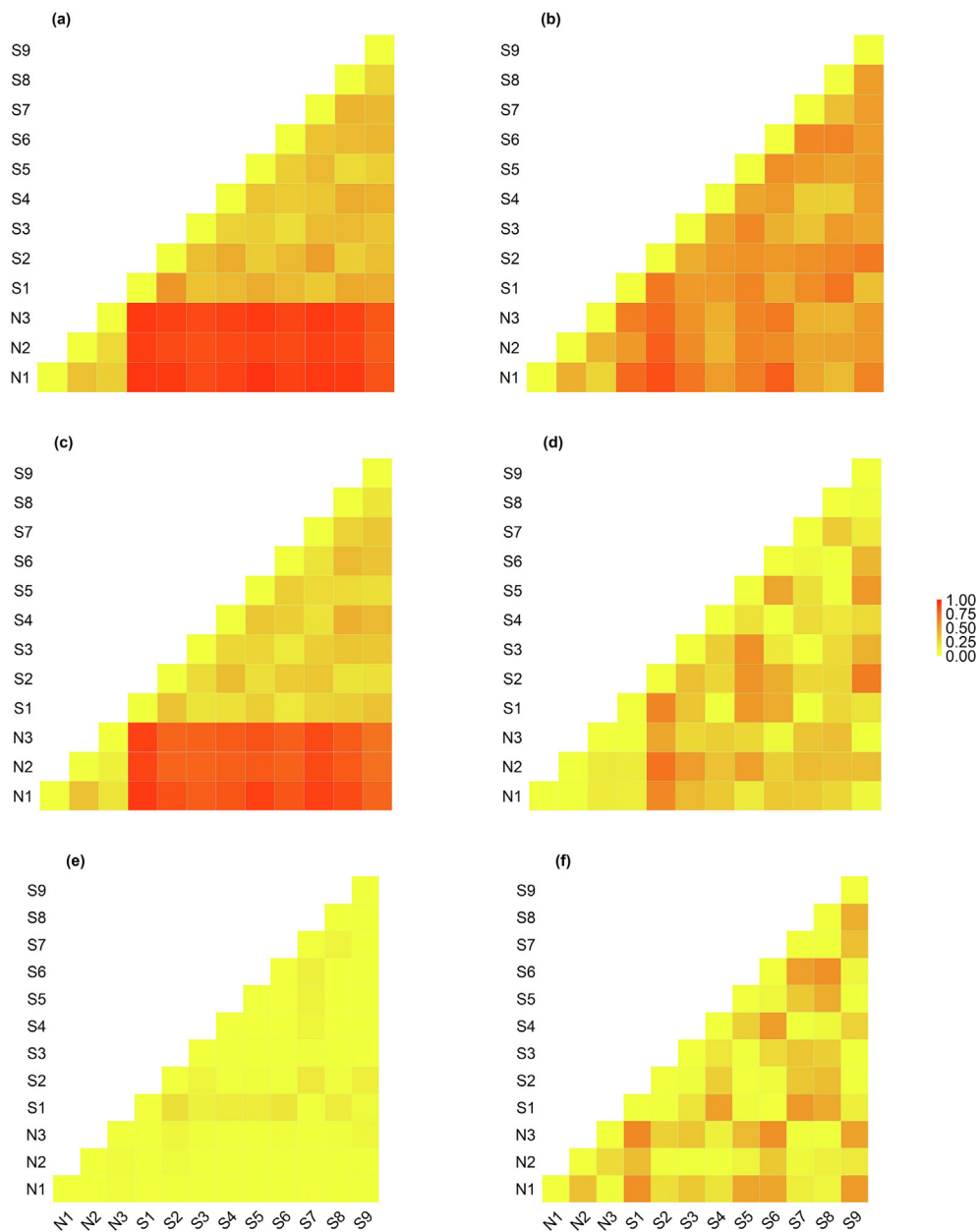


Figure 6. Heatmap showing taxonomic (a, c, e) and functional (b, d, f) beta diversity between sites for bird communities occurring in the sugarcane and savanna sites in north-eastern Eswatini: (a) total taxonomic beta diversity (β_{sor}); (b) functional beta diversity (β_{sor}); (c) taxonomic turnover (β_{sim}); (d) functional turnover; (e) taxonomic nestedness (β_{nes}); and (f) functional nestedness. N1–N3 represent the three sites in savanna and S1–S9 represent the nine sites in the sugarcane.

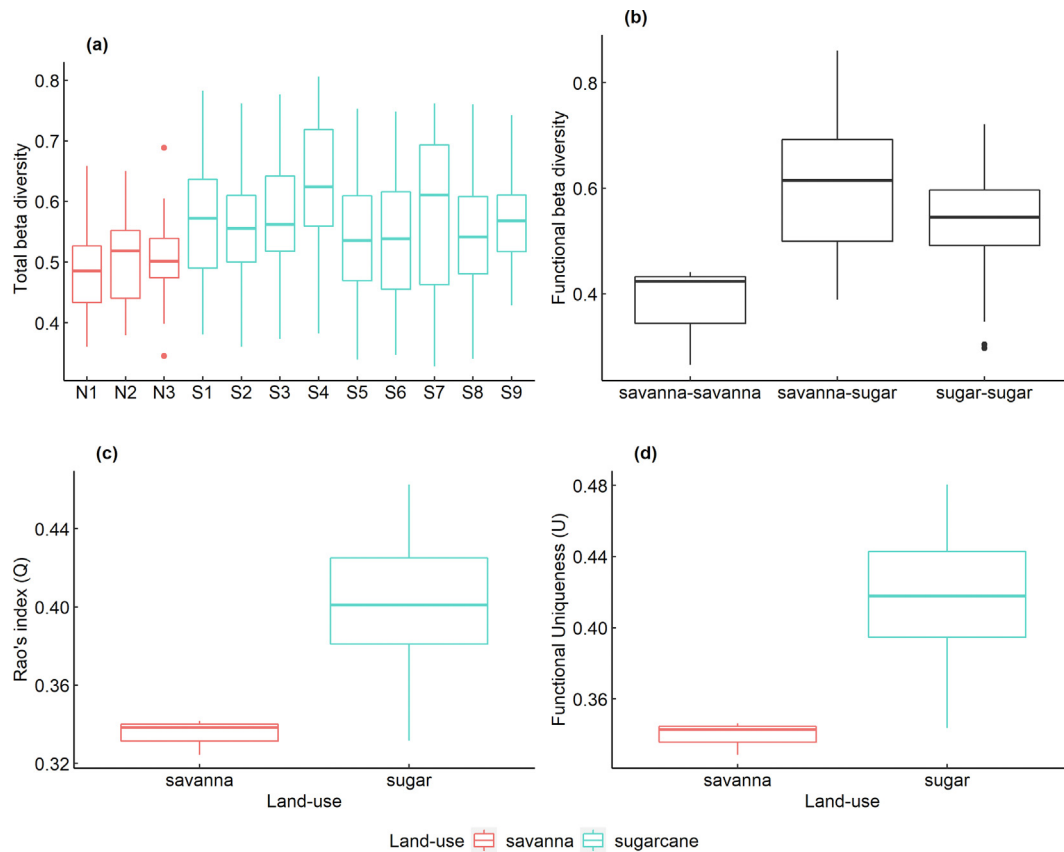


Figure 7. Boxplots showing: (a) total (temporal) taxonomic beta diversity of bird species recorded at each site in savanna (N1–N3) and sugarcane (S1–S9); (b) functional beta diversity between and within sugarcane and savanna sites; (c) functional alpha diversity (Rao's Index Q); and (d) community-level functional uniqueness index (U) of the bird communities surveyed in the two land-uses; sugarcane and savanna in north-eastern Eswatini.

Table 7. Dunn's Multiple comparison test for functional beta diversity between and within the savanna and sugarcane land-uses; sav = savanna, sug = sugarcane.

comparison	Z	p.unadj	p.adj
sav-sav vs sav-sug	-2.739	0.006	0.018
sav-sav vs sug-sug	-1.972	0.049	0.146
sav-sug vs sug-sug	1.937	0.058	0.175

sugarcane. The increase in species richness in the savanna in the wet season might be due to the influx of summer migrants as well as the availability of food during the wet season due to increase in plant biomass, and the insects that feed on them, as compared to the dry season. On the contrary, the lack of a difference in richness and diversity between seasons in sugarcane might be because these fields are continuously irrigated, reducing any differences in available food resources between the seasons.

Despite the spatial and temporal variability created by different growth stages of sugarcane, it is well documented that reductions in the structural complexity of the habitat and in heterogeneity caused by intensification of agricultural areas are factors that reduce biodiversity (Benton et al., 2003; Stanton et al., 2020). Sugarcane fields are an example of such a system. Although we found that this variability provided habitat for some bird species, particularly ground-foragers, both species richness and diversity were consistently lower in fields of all stages of sugarcane growth, compared to the adjacent savannas.

5. Conclusion

Our study demonstrates that while native savanna has greater richness and diversity of birds and supports a distinct avian community from

that occurring in sugarcane fields, the temporal and spatial variability within sugarcane fields contributes to high taxonomic and functional beta diversity, and functional uniqueness in this land use, likely increasing the number of avian species that sugarcane fields can support. We therefore suggest that sugarcane plantations and other intensely farmed croplands, with similar heterogeneity in crop structure, may be of some value to biodiversity conservation, and should therefore be incorporated into regional conservation management plans.

Declarations

Author contribution statement

Sifiso M. Lukhele: Performed the experiments; Analyzed and interpreted the data; Wrote the paper.

Julie Teresa Shapiro; Muzi D. Sibiyi; Robert J. Fletcher Jr: Analyzed and interpreted the data; Wrote the paper.

Themb'alilahlwa A.M. Mahlaba; Robert A. McCleery: Contributed reagents, materials, analysis tools or data; Wrote the paper.

Ara Monadjem: Conceived and designed the experiments; Analyzed and interpreted the data; Wrote the paper.

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Data availability statement

Data will be made available on request.

Declaration of interests statement

The authors declare no conflict of interest.

Additional information

No additional information is available for this paper.

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