



Abandoned fields show higher insectivorous Bat species and functional diversity than forest fragments in a communal land area of the Eastern Cape, South Africa

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Abstract

Deagrarianisation is a global phenomenon with high potential for both carbon sequestration and biodiversity conservation. Work on this topic has focused on plant succession and associated plant diversity, but few studies have considered faunal communities, particularly in Africa. We used passive acoustic monitoring to record insectivorous bat communities within forest fragments and former fields under communal land tenure in the Transkei region (Eastern Cape Province) of South Africa. Insectivorous bat diversity in fields, abandoned in the 1960s to 1980s, resembling late stages of succession, were compared to fragments of Transkei Coastal Scarp Forest embedded within the landscape. We found that former fields hosted 14 species from 11 genera, comprising greater species richness, activity, Shannon-Weiner diversity, and functional diversity, irrespective of age, compared to forest fragments, which hosted nine species from seven genera. Furthermore, former fields exhibited comparable species richness to, and higher functional diversity than, three large neighbouring intact Transkei Scarp forests. Interestingly, the time since cultivation had ceased (35–64 years ago) had no significant effect on species and functional diversity. Former fields exhibited extensive invasion by *Lantana camara* (an alien shrub), and the indigenous pioneer tree *Vachellia karoo*, but nonetheless these landscapes have conservation value as they are diverse in both terms of insectivorous bat species and function. Mechanisms to enhance both biodiversity conservation; and the utility of the land for impoverished local communities, should be considered for former fields in tandem with forest patches, which remain important for bat roosting and foraging ecology, especially for specialist species.

Keywords Agricultural transition · Succession · Savanna-woodland · Foraging guild · Bat acoustic monitoring · Functional diversity · Crop abandonment

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Extended author information available on the last page of the article

Introduction

“Deagrarianisation” is the process whereby agricultural fields, often under communal land tenure, are no longer planted for crops (Shackleton et al. 2013; Hebinck et al. 2018). Although there has been a net positive increase in agricultural area globally, deagrarianisation has been a feature in developed countries in Western Europe and North America, which together showed a total reduction of 3.79 million km² in agricultural area from 1961 to 2011. By contrast, developing regions such as Asia, Africa, and Latin America have been increasing in agricultural land-use (Li and Li 2017), but with some areas showing increasing rates of abandonment after major social-ecological transitions (Shackleton et al. 2013; Hebinck et al. 2018). There is some concern that farmland abandonment could reduce landscape diversity and biodiversity, especially in Europe, where a long history of agriculture has led to occupation by species, specifically adapted to farmland (Bignal and McCracken 1996; Queiroz et al. 2014). But other studies view land-abandonment as a means for natural ecosystem restoration through ecological succession (Aide and Grau 2004) and rewilding or reforestation (Navarro and Pereira 2012; Corlett 2016), with such changes supporting biodiversity and the provision of important ecosystem services like carbon sequestration. For example, Strassburg et al. (2020) showed that restoring 15% of converted lands globally in priority areas could avoid 60% of expected extinctions for mammalian, amphibian, and bird species while sequestering 299 gigatonnes of CO₂. This amounts to 30% of the total CO₂ increase in the atmosphere (14% of total emissions), since the advent of the Anthropocene.

Outside of the “Global North”, southern and northern Africa can provide useful insights into deagrarianisation, as they are the two regions in Africa which generally have experienced a decline in agricultural area, rather than an increase (Li and Li 2017). South Africa has exhibited a net decrease (−2.1%, 347,267 hectares) in cultivated land between 1990 and 2014 and an estimated six-fold increase in “naturalised or rewilded” former fields (approximately 2 million hectares), with the Eastern Cape Province (hereafter Eastern Cape), in particular, exhibiting a large increase in natural or semi-natural land cover (Statistics South Africa 2020). In the Transkei, a communal land tenure area of the Eastern Cape, this trend is particularly common (Shackleton et al. 2019), with the area of former fields equal to that of active fields by 2010 (Blair et al. 2018). Several social-ecological factors have driven deagrarianisation in the Transkei, including reduced livestock ownership and reduced governmental support for dipping; the introduction of social security grants; altered community structures arising from post-apartheid migration and urbanisation; human-wildlife conflicts; and changing environmental conditions among others (Andrew and Fox 2004; Shackleton et al. 2013, 2019).

Studies on the effects of deagrarianisation on biodiversity in South Africa have centred on plant community dynamics within the Eastern Cape (Shackleton et al. 2013; Hebinck et al. 2018; Njwaxu and Shackleton 2019). While these fields have been abandoned in terms of cropping, local communities continue to rely on the former fields for cattle grazing and informal harvesting of natural products like fuelwood and medicinal plants (Berliner 2011; Njwaxu and Shackleton 2019; Shackleton et al. 2019). Despite this use, studies at Willowvale, in the Transkei, indicate an increase in woody biomass (although still low in comparison to forest fragments) and species richness (similar to forest fragments) with increasing age since cropping abandonment (Shackleton et al. 2013; Njwaxu and Shackleton 2019). The regeneration capacity is likely to be dependent on pre- and post-anthropogenic

disturbance intensities, post-abandonment natural vegetation contributions (i.e., seed banks and native seed dispersers), and the duration of the pioneer stage and impacts of invasive species (Shackleton et al. 2013). By comparison, the effects of deagrarianisation on faunal communities is poorly documented in South Africa.

Bats provide a range of ecological functions as seed dispersers and arthropod pest suppressors (Taylor et al. 2018), are easily monitored with passive acoustic techniques (Jones et al. 2009) and display plasticity towards landscape modifications (Parrotta et al. 1997; Linden et al. 2014). Visual identification of bats in field is difficult due to their nocturnal and flying nature and while active capture provides basic community data and species verifications, not all locations are easily sampled (Teets et al. 2019). Passive acoustic monitoring provides an alternative that allows for species identification and wide-range deployment to enhance bat monitoring (Jones et al. 2009). With this neotropical studies have monitored phyllostomid (leaf-nosed) bat assemblages in post-anthropogenically disturbed environments such as slash-and-burn fields, agricultural fields, and fragmented forest matrices (Castro-Luna et al. 2007; Avila-Cabadilla et al. 2009; Farneda et al. 2022), and report variable responses of this ecologically-diverse family (which include, insectivores, carnivores and frugivores), to ecological succession and restoration post-anthropogenic change. For example, Castro-Luna et al. (2007) discuss that bat abundance is driven by vegetation variables over landscape variables, whereas Avila-Cabadilla et al. (2009) show that later successional stages exhibit greater species richness and rare species presence. These studies do not focus specifically on insectivorous bats and moreover suggest that more research is required to properly assess the implications of ecological succession on bat species assemblages.

During the Last Glacial Maximum, a low climate change footprint in eastern South Africa prevented population declines of insectivorous bats, where scarp forests, in particular, offered refuge (Moir et al. 2020b). Thus these areas now display a high diversity of bats (Moir et al. 2020b). Based on a species' preferred roosting and foraging habitats, insectivorous bats are split into three guilds: clutter (found in dense vegetated areas), clutter-edge (found at the edges of dense vegetation and canopy gaps) and open-air foragers (found in areas absent of vegetation) (Norberg and Rayner 1987; Fenton 1990; Weier et al. 2018;). The guilds are further differentiated by their echolocation strategies (high-duty cycles versus low-duty cycles) and their eco-morphological characteristics, low wing loading for increased manoeuvrability in dense vegetation (clutter foragers) versus high wing loading for speed and agility (open-air foragers) (Norberg and Rayner 1987; Fenton 1990; Schnitzler and Kalko 2001). Clutter-edge foragers share similarities between both clutter and open-air foraging guilds, exhibiting a mid-range wingspan and mixed echolocation signals (Schnitzler and Kalko 1998, 2001).

As bats are known to be sensitive to environmental changes, landscape changes will likely result in community and behaviour shifts due to differential roosting and foraging preferences (Jones et al. 2009; Monadjem et al. 2020). Structural changes in vegetation can also have a significant impact on population dynamics, particularly for clutter foragers which are more susceptible to habitat loss and fragmentation as specialist species (Jones et al. 2009; Cory-Toussaint and Taylor 2022). Bats (and clutter foragers in particular) are considered vulnerable to the ongoing impacts of climate change on landscape functioning (Opdam et al. 2009) and habitat loss due to disturbance (Jung and Threlfall 2016; Cory-Toussaint and Taylor 2022).

In this study, we aim to evaluate the diversity and activity of insectivorous bats in former agricultural fields as compared to forest fragments in the Transkei region of South Africa. We hypothesised that; (1) bat species and functional diversity would increase with length of time since field abandonment, as vegetation and landscape complexity increase with ecological succession (Avila-Cabadilla et al. 2009); (2) the bat activity, number of echolocation pulses, would increase at later successional stages with an increase in niche availability; and (3) clutter foragers would be limited to forest fragment sites (Avila-Cabadilla et al. 2009; Clement 2024).

Methods

Study site

The study acoustically surveyed two fragments of Transkei coastal scarp forest (defined in Mucina and Rutherford 2006) and six former crop fields near the mouth of the Qora River, south-east of the town of Willowvale (32.26 °S; 28.50 °E) in the Transkei area of the Eastern Cape, South Africa (Fig. 1). The area lies within the Maputaland-Pondoland-Albany biodiversity hotspot, a centre of high endemism and species diversity, which is a priority area identified by Strassburg et al. (2020) in terms of carbon sequestration and reversing the extinction debt. The greater region is characterized by a mosaic of Transkei coastal scarp forest, thornveld, dune thicket, and grassland landscapes (von Maltitz et al. 2003; Mucina and Rutherford 2006; Berliner 2011). In the area, field cover has declined from 12.5% in 1961 to 2.7% in 2009, with a peak in field abandonment during the transition to democracy in the early 1990s (Shackleton et al. 2013), and trees and shrubs have started to naturally regenerate in abandoned field.

Njwaxu and Shackleton (2019) had previously assessed vegetation succession in 43 former fields with different abandonment ages and compared it to seven forest fragments in study area. Based on their previous work, we selected two sites from different decades of abandonment, 1960s, 1970s and 1980s ($n=6$), for passive acoustic monitoring as well as two forest fragments (Figs. 1 and 2). These covered a temporal range of 35–64 years as assessed by Njwaxu and Shackleton (2019). The fields are located within a matrix of dispersed rural villages and homesteads, sand roads, and forest fragments (Shackleton et al. 2013; Njwaxu and Shackleton 2019) and were on average 2.9 km apart with the closest and furthest sites being 300 m and 8.1 km apart, respectively (Online Resource 1: Table S1, S2). While abandoned in terms of cropping, these fields remain utilised by the local community for informal harvesting of non-timber forest products and cattle grazing (Njwaxu and Shackleton 2019; Fig. 2). Further, two large intact forests, Manubi, and Dwesa, surveyed by Moir et al. (2020a) were compared to these sites.

Permits and ethical clearance

Sampling was conducted under a permit issued by the Economic Development Environmental Affairs and Tourism Department of the Eastern Cape Province (HO/RSH/11/2023) and Sect. 20 authorisation from the Department of Agricultural, Land Reform and Rural Development. Ethical clearance was obtained through the Stellenbosch University Animal

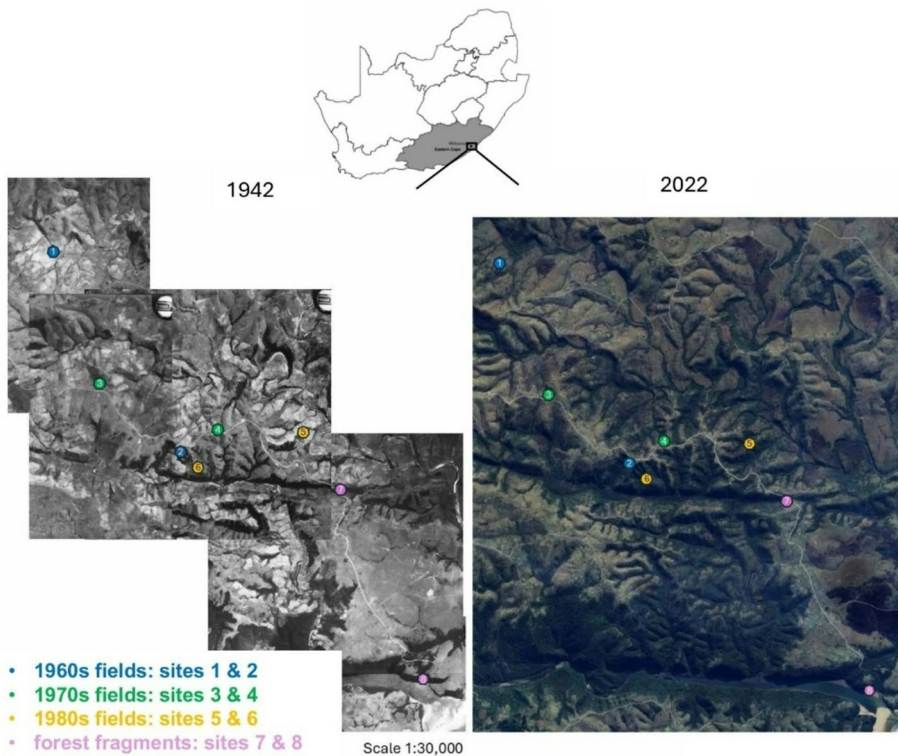


Fig. 1 Study site locations within the Willowvale area, Eastern Cape Province, South Africa. Including aerial photos from 1942 and satellite images from 2022 showing the land-use of the study sites over time. The dots and numbers show our field plots including: 1 & 2 (fields abandoned in the 1960s), 3 & 4 (fields abandoned in the 1970s), 5 & 6 (fields abandoned in the 1980s), and 7 & 8 (forest fragment sites)

Care and Use Committee (ACU-2023028082) and landowner permission was obtained from the local Chief (LOA202309051) and headman (LOA20230905 2) of the area.

Survey methods

Four Wildlife Acoustics Song Meter SM4BAT (with SMM-U1 microphones) and four Song Meter SM2BAT+ (with SMX-US microphones) full spectrum ultrasonic monitors were deployed across the eight sites over two separate sampling periods in 2023 (12 sampling nights; 96 detector nights); one in the austral autumn (March 24 — April 3) where sites were surveyed for seven nights and the second in the austral spring (5 — 10 September) where sites were surveyed for five nights. To reach sampling saturation in this region, six to seven nights is deemed sufficient (Moir et al. 2020a) with one sampling night being comprised of multiple detector nights since eight detectors were deployed simultaneously (Law et al. 2015). Only five sampling nights were obtained in spring due to inclement weather conditions. Additionally, sampling was conducted under minimal lunar illumination (Appel et al. 2017) and acoustic sampling nights that had strong winds (>4.47 m/s; O’Farrell et al. 1967)

Fig. 2 General habitat structure of eight sites for passive acoustic monitoring of insectivorous bats. Former fields: 1 & 2 (abandoned in 1960 s); 2 & 3 (abandoned in 1970 s); 4 & 5 (abandoned in 1980 s); 6 & 7 (Forest fragments)



or had precipitation exceed 3 mm (following Fischer et al. 2009) were discarded during analysis, as both reduce bat foraging activity (O'Farrell et al. 1967; Stebbings 1968; Appel et al. 2019).

We used two different models of acoustic monitoring devices but we confirmed no statistical difference between them (Online Resource 1: Table S3). Both monitor types were set to trigger at a minimum of 12 kHz, with 384 kHz sample rate and 12dB gain in full spectrum (see Online Resource 1: Table S4) and scheduled to record from a half hour prior to sunset until a half hour post sunrise (approximately 14 recording hours), following Moir et al. (2020a) and Kunz and Parsons (2009). Microphones were placed 1.5–2 m above the ground and positioned towards flyways to enhance audio capture and mitigate call attenuation and echoes (Weller and Zabel 2002). Sampling sites were separated by a minimum distance of 250–450 m to mitigate simultaneously capturing calls from the same individual (Moir et al. 2020a; Law et al. 2015). However, as ultrasonic microphones have a range of roughly 30 m (Agranat 2014), the likelihood of capturing the same bat simultaneously is improbable (Law et al. 2015).

Acoustic analyses

Echolocation calls were visualised and measured in Wildlife Acoustics Kaleidoscope Pro software (version 4.5.5). A call was defined as at least two recorded pulses within < 1 s of silence between (Fenton 1970). A total of 52,814 audio files were recorded over the autumn and spring sampling periods, of which 1,185 unidentifiable calls and 47,073 noise files were removed. A total of 4,556 echolocation calls were manually identified to species level using spectrogram visualisation, using zero crossing call parameters and regional call libraries from the eastern regions of South Africa (Taylor et al. 2013; Moir et al. 2020a).

Key call parameters used for species identification were characteristic frequency (F_c), maximum (F_{max}) and minimum frequency (F_{min}), duration (Dur), and knee frequency (F_k). Due to the overlapping F_c parameters between *Tadarida aegyptiaca* and *Mops pumilus*, characteristic frequency calls that ranged between 18 and 22 kHz were assigned to *T. aegyptiaca* and the 23–27.7 kHz range were assigned to *M. pumilus*, following the mean F_c stipulated in Monadjem et al. (2020). To differentiate between *Scotophilus dinganii* and *Laephotis* cf. *botswanae*, *S. dinganii* was assigned a call duration between 3.5 and 4.6 ms and a knee frequency of 36–37 kHz, while *L. cf. botswanae* was assigned a call duration of 2–3 ms and a maximum knee frequency of 35 kHz (Taylor et al. 2013; Moir et al. 2020a). Lastly, *Chaerephon ansorgei* and *Cnephaeus hottentotus* were removed as potential species identifications based on their geographic distribution profiles (Monadjem et al. 2020) and lack of recording and active capture in the general study region (Moir et al. 2020a).

Activity was measured both as the total number of bat echolocation passes (henceforth referred to as ‘passes’) per night and the average number of passes recorded per hour per night. Species specific activity was standardised to Activity Index (AI) (the presence of species per one minute time intervals, following Miller (2001)). Nocturnal activity time graphs were constructed based on the number of passes per hour per night for autumn and spring separately, and for the pooled data.

Statistical analysis

Generalised linear models and generalised least squared models were used to test for significant predictors of Species Richness, Pielou’s Evenness, Shannon-Weiner diversity, and activity (total passes/night; average passes/hour/night in R software (version 4.3.1)). Predictor variables included distance to the nearest water body (m), distance to the nearest building (m), distance to the nearest road (m), distance to the nearest forest fragment (m), and cardinal direction (Online Resource 1: Table S5 for values). Predictor correlation tests were run using the “corr.test” function in the “psych” package (version 2.5.6). Models were selected based on Akaike’s information criterion (AIC) with $\Delta AIC_c \leq 2$ models considered to be strongly competing (Burnham & Anderson 2002; Meyer et al., 2008) using the function “dredge” in the “MuMIn” package (version 1.47.5). Depending on the normality of the data, either an ANOVA or a Kruskal-Wallis test was performed. Additionally, logistic regression models were run to test for significant predictors of foraging guild and three species’ presence using packages “lme4” (version 1.1.34). *Pipistrellus hesperidus*, *Laephotis capensis*, and *Rhinolophus acrotis*, (previously *R. clivosus*, Uvizi et al. 2024) were chosen as the most actively dominant species across sites. Since acoustic sampling cannot differentiate individual bats, bat activity was used as a proxy for bat abundance (Froidevaux et al.

2019; Barré et al. 2019). We also conducted spatial autocorrelation tested using the “ape” (version 5.7.1) and “sf” (version 1.0.15) package following Moir et al. (2021), and found no evidence of autocorrelation between sites (Online Resource 1: Table S6). Moir et al. (2021) found similar results in the Eastern Cape forests; the high dispersal ability of mollosids and some vespers found in this study often preclude much beta diversity (or spatial autocorrelation) at small geographical scales of km’s to tens of km’s (Foord et al. 2018; Monadjem et al. 2023; Taylor et al. 2025), which may contribute to the lack of spatial autocorrelation.

Species diversity was quantified by species richness, Shannon-Weiner diversity, Pielou’s evenness and four functional diversity indices: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and functional dispersion (FDis). Firstly, species accumulation curve estimates were generated across detector nights using EstimateS software (version 9.1.0) (Colwell 2013); Chao (1987) to assess the species sampling saturation for sites (Moreno and Halffter 2000). Each site category used a total of 22 detector nights for analysis after pooling 11 sampling nights from each site. Shannon-Weiner diversity and Pielou Evenness estimates were then calculated using the package “vegan” (version 2.6.4) (Oksanen et al. 2022). Lastly, functional diversity indices were calculated using the “FD” package (version 1.0.12.3) (Laliberté and Legendre 2010) following Moir et al. (2021), using the same functional traits. We chose the following traits because they are the most frequently adopted in ecological bat studies and they play key functional roles in the detection of clutter and prey, conspecific and heterospecific identification, manoeuvrability in suitable foraging habitat, and dispersal and flight ability (Siemers and Schnitzler 2004; Moir et al. 2021; Monadjem et al. 2023): echolocation call type, characteristic frequency, forearm length, aspect ratio, and wing loading (Online Resource 1: Table S7). Trait values were obtained from Moir et al. (2020a) and combined with the characteristic frequency and echolocation call type recorded during our passive acoustic sampling. Continuous traits were standardized to a mean of zero and standard deviation of one to allow comparison of their relative effects (Farneda et al. 2015). Lastly, to investigate relationships between functional metrics and site categories, mixed linear effect models using the package “glmmTMB” (version 1.1.7) (Brooks et al. 2017) were used with site as a random variable.

Results

Sampling effort and species inventory

Fourteen species belonging to four families were detected in the study area using passive acoustic monitoring (Table 1). Species richness estimates (Chao 1 mean) (Fig. 3) demonstrated sampling saturation was achieved for all categories, with plateaus being reached between 11 and 13 detector nights. Former fields abandoned in the 1960s and 1970s reached saturation at 15 sampling nights (and had the exact same saturation curve), whereas field abandoned in the 1980s and forest fragments reached sampling saturation after 13 and 16 detector nights, respectively (Fig. 3). The SR estimates showed that 15 species were predicted to be present in fields abandoned in the 1960s and 1970s, while 11 and eight species were predicted for fields abandoned in the 1980s and for forest fragments, respectively. These expected results closely mirror our realised species presence records (Table 1). More specifically, *R. acrotis*, *Otomops martiensseni*, *Mops midas*, *Miniopterus fraterculus*,

Table 1 Insectivorous Bat species from three guilds (Open-air, CE - Clutter-edge, and Clutter) recorded in former agricultural fields with different abandonment ages (1960s, 70s and 80s) and forest fragments. Species for nearby large Transkei scarp forests (Silaka, Dwesa, and Manubi) from Moir et al. (2020a) are provided for comparison. Areas marked with an asterisk indicate species presence for those sites

Family and species	Foraging guild	Former fields with abandonment different ages			Forest fragment	Large intact Transkei Coastal Scarp Forest patches (from Moir et al. 2020a)		
		1980s	1970s	1960s		Silaka	Dwesa	Manubi
Rhinolophidae								
<i>Rhinolophus acrotis</i>	Clutter	*	*	*		*		*
<i>R. swinnyi</i>	Clutter					*	*	
Molossidae								
<i>Mops pumilus</i>	Open-air	*	*	*	*		*	
<i>M. condylurus</i>	Open-air	*	*	*	*			
<i>M. midas</i>	Open-air	*		*	*			
<i>Otomops martiensseni</i>	Open-air	*	*	*				*
<i>Tadarida aegyptiaca</i>	Open-air	*	*	*	*	*	*	*
Miniopteridae								
<i>Miniopterus fraterculus</i>	CE		*	*		*	*	*
<i>M. natalensis</i>	CE	*	*	*	*	*	*	*
Vespertilionidae								
<i>Afronycteris nanusa</i>	CE	*	*		*	*		*
<i>Cnephaeus hottentotus</i>	CE							*
<i>Pipistrellus hesperidus</i>	CE	*	*		*	*		*
<i>Scotophilus dinganii</i>	CE	*	*		*	*		*
<i>Laephotis</i> cf. <i>botswanae</i>	CE							*
<i>L. capensis</i>	CE	*	*		*	*		*
<i>Myotis tricolor</i>	CE	*			*	*		*
<i>Neoromicia hlandzeni</i>	CE & Clutter	*	*	*				*

Myotis tricolor, and *Neoromicia hlandzeni* (formally *N. anchietae*) were absent from forest fragments but were each detected in multiple former fields with different abandonment ages.

Species richness, diversity, and evenness.

The former fields exhibited a greater species richness, Shannon-Weiner diversity, and Pielou's evenness compared to the forest fragments (Table 2). More specifically, fourteen species were recorded for those abandoned in the 1960s, 11 for 1970s, and 13 for 1980s, of which all were significantly greater than forest fragments where nine species were recorded (ANOVA; 1960s: $t_{3,95} = 3.54$, $P < 0.0001$; 1970s: $t_{3,95} = 2.43$, $P < 0.05$; 1980s: $t_{3,95} = 5.23$, $P < 0.0001$). Similarly, Shannon-Weiner mean diversity and Pielou's evenness was greater in former fields, and was highest in former fields abandoned in the 1960s, $\bar{X} = 0.89 \pm 0.49$ and 1980s $\bar{X} = 0.40 \pm 0.19$, respectively (Online Resource 1: Table S8). The only significant difference between former fields, for all three metrics, was between those abandoned in the 1970s as compared to those abandoned in the 1980s, with species richness being (13 vs. 11) diversity ($\bar{X} = 0.75 \pm 0.40$ vs. $\bar{X} = 1.06 \pm 0.42$) and evenness ($\bar{X} = 0.40 \pm 0.19$ vs. $\bar{X} = 0.28 \pm 0.15$) besieging significantly greater in fields abandoned in the 1980s compared to the 1970s (Online Resource 1: Table S8).

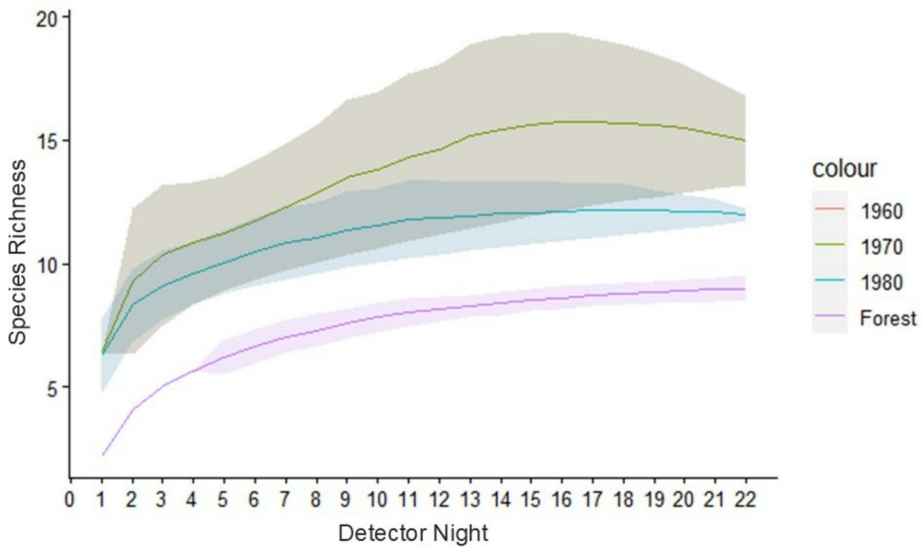


Fig. 3 Species richness estimates across detector nights were calculated in EstimateS (Colwell 2013) for pooled data from former fields abandoned in the 1960s, 1970s, 1980s and forest fragments. Standard deviations are indicated by the shaded area and the species accumulation curves derived for former fields abandoned in the 1960s and 1970s exhibit the exact same trajectory, and thus appears as a single green line

Table 2 Total acoustic nights and total Bat passes, species richness (SR), average Shannon-Weiner diversity (H'), average piélou's Evenness, and summed activity index (AI) (Miller 2001) of species per former field category (abandoned in the 1960s, 1970s, and 1980s) and forest fragment sites

	Total acoustic nights	SR	Shannon diversity (H')	Pielou's evenness	Mean total bat passes/night (total bat passes)	Mean bat passes recording/hour	Mean activity (mean AI)
Former fields							
1980s	24	13	1.06	0.40	69.71 (1673)	6.00	1.98
1970s	26	11	0.75	0.28	37.69 (934)	2.27	1.05
1960s	25	14	0.89	0.34	43.00 (1073)	2.56	1.40
Forest fragments	24	9	0.50	0.19	16.71 (401)	1.04	0.81

Based on saturated GLM models ($\Delta AICc \leq 2$) only three predictors had a significant effect on the species richness, diversity, or evenness of insectivorous bats; distance to nearest road and building respectively; and cardinal direction (Online Resource 1: Table S9). Distance to nearest building and nearest road negatively and positively impacted species richness, respectively (ANOVA: $t_{6,95} = 9.18$, $P < 0.05$; $t_{6,95} = 8.95$, $P < 0.05$). However, it is important to note that distance to nearest building and nearest road were found to be highly correlated with each other (Online Resource 1: Table S10). Cardinal direction was the only significant predictor for both diversity and evenness, with west north-west (site 2; 1960) and west facing (site 6; 1980) sloped sites having the greatest diversity values (Fig. 4) yet

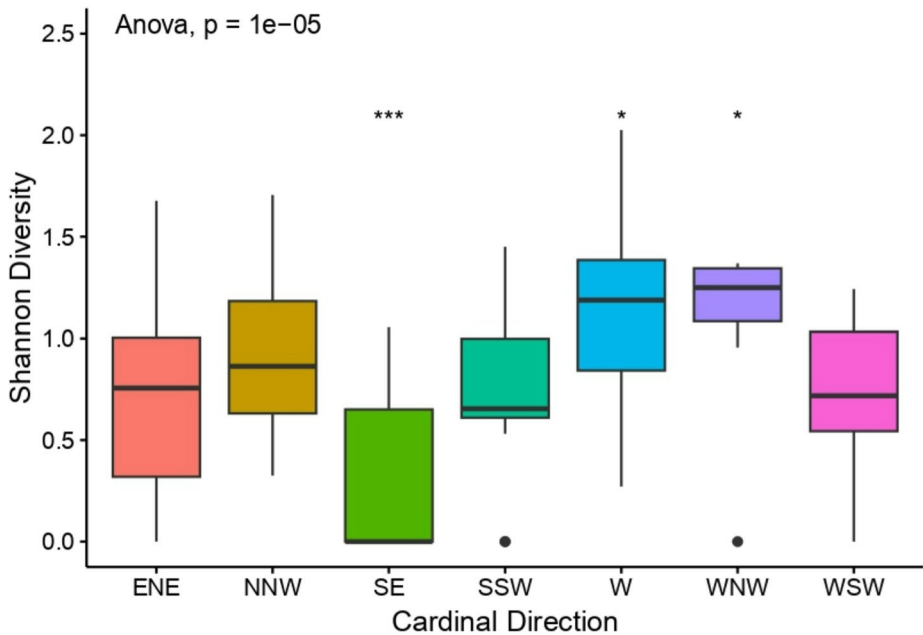


Fig. 4 Shannon-Weiner Diversity for insectivorous bat species across site cardinal direction. Significant differences are identified with an asterisk. From left to right: East North-East (site 1); North North-West (site 4 & 5); Southeast (site 8); South South-West (site 7); West (site 6); West North-West (site 2); West South-West (site 3)

comparable to each other (ANOVA: diversity $t_{6,95} = -0.21$, $P=0.83$) and south-east facing slopes had the lowest diversity (Online Resource 1: Table S9).

Bat activity

Bat activity was similarly greatest in former fields and lowest in forest fragments (Table 2). Both total passes per night ($\bar{X} = 16.71 \pm 28.09$) and mean passes per hour ($\bar{X} = 1.04 \pm 2.23$) were lowest in forest fragments (Table 2). Total passes were highest in former fields abandoned in the 1980s as compared to those abandoned in the 1970s and 60s (1980 — 1960: $t = -2.22$, $P=0.03$; 1980 — 1970: $t = -2.5$, $P=0.01$). Across all former fields, *L. capensis*, *M. natalensis*, and *P. hesperidus* were the three most active species (*L. capensis*: AI=26.94; *M. natalensis* AI=16.71; *P. hesperidus*: AI=10.12) (Fig. 5). However, looking at each site in isolation, *P. hesperidus* (AI=5.25) was the most active species in the forest fragment, *R. acrotis* (AI=3.08) in former fields from the 1970s, and was *L. capensis* most active in fields abandoned in the 1960s and 1980 (Fig. 5). *Rhinolophus acrotis* was the only species, of the three investigated, that was influenced by the predictor variables. *Rhinolophus acrotis* presence was positively impacted by increasing proximity to roads and forest fragments (GLM: Forest fragment: $z=2.078$, $P<0.05$; Road: $z=3.108$, $P<0.001$), but presence decreased with proximity to the nearest building (GLM: $z = -3.299$, $P<0.0001$).

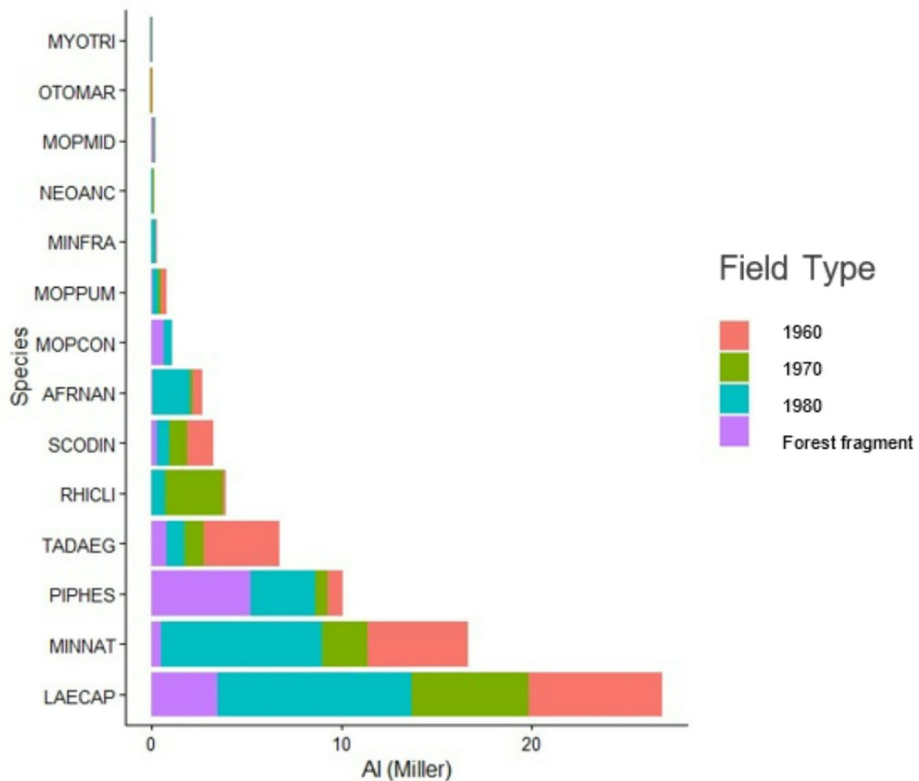


Fig. 5 A comparison between the summed activity indices (AI - Miller 2001) of recorded insectivorous bat species across former fields and forest fragments (pooled data)

Foraging guild analysis

At the guild-level only field abandonment age, proximity to buildings, and proximity to roads significantly impacted guild presence (Online Resource 1: Table S11). For open-air guilds, field abandonment age positively impacted open-air species presence, as did proximity to roads, for both open-air and clutter foragers across site categories (Open-air: $z=2.588$, $P<0.001$; Clutter: $z=2.533$, $P<0.05$). Clutter-edge species were only negatively impacted by proximity to buildings (Clutter-Edge: $z=-2.106$, $P<0.05$) as with open-air and clutter foragers (Open-Air: $z=-2.149$, $P<0.05$; Clutter: $z=-2.99$, $P<0.05$). Again, it is important to note that distance to nearest roads and buildings are positively correlated (Online Resource 1: Table S10).

Functional diversity indices

Functional diversity values varied across former field categories and forest fragments - depending on the indices analysed (Table 3). Functional richness was comparable across former fields with different abandonment ages but was significantly lower for forest frag-

Table 3 Species richness and mean functional indices (functional richness, functional evenness, functional divergence, and functional dispersion) for the surveyed sites (former fields with different abandonment ages and forest fragments) and nearby Transkei coastal scarp Forests, Silaka, Manubi, and Dwesa (Moir et al. 2021), are provided for comparison

	Species richness	Functional richness	Functional evenness	Functional divergence	Functional dispersion
Former fields					
1960s	14	5.579	0.159	0.654	0.707
1970s	12	5.114	0.457	0.713	1.194
1980s	13	6.269	0.447	0.630	0.384
Forest fragments	9	0.594	0.505	0.772	0.608
Transkei Coastal Scarp	10	0.237	0.261	0.883	0.763
Forests (from Moir et al. 2021)	12	0.565	0.479	0.759	0.729
	14	1.208	0.253	0.852	0.569
Silaka					
Dwesa					
Manubi					

ments (GLM; 1960s: $z = -2.689$; $P < 0.05$; 1970s: $z = -2.657$; $P < 0.05$; 1980s: $z = -2.272$; $P < 0.05$) (Online Resource: Table S12). Whereas functional evenness values were lowest in former fields abandoned in the 1960s (GLM; 1970s: $z = -3.219$; $P < 0.01$; 1980s: $z = -3.173$; $P < 0.01$; $z = -3.417$; $P < 0.01$), functional dispersion was lowest in former fields abandoned in the 1980s (GLM: $z = -2.479$; $P < 0.05$). Lastly, functional divergence values were comparable across all sites (former fields with different abandonment ages and forest fragments) (Online Resource: Table S12).

Discussion

Former fields in the Willowvale area provide suitable habitat for 14 insectivorous bat species from 11 genera and high functional diversity compared both to forest fragments and to large intact forests (Moir et al. 2021). Clutter-edge and open-air foraging guilds are represented by eight and five species, respectively. The number of clutter-edge bat species (Miniopteridae and Vespertilionidae) recorded in former fields abandoned in the 1960s is close to that of Manubi forest (eight versus ten species) - the most diverse large Transkei Scarp Forest patch in the region (Moir et al. 2020a). However, open-air forager diversity is much higher in former fields of all abandonment ages compared to the forest fragments. Primarily as a consequence of the high diversity and activity of open-air foragers, the functional richness and functional dispersion of former fields at Willowvale were far higher than that of intact forests, and functional evenness was also high. It should be noted that open-air species presence may have been lower in Moir et al. (2020a) due to the masking effects of forest canopy causing call attenuation from bats flying above the canopy. Regardless, both the high functional diversity of, and the similarity in species composition between the former fields and nearby intact forests highlights the conservation potential of former fields.

Contrary to our predictions, bat species were not strongly influenced by the length of time since abandonment of former fields. This contrasts with plant species richness in the which increases significantly with time since abandonment in former fields in the same region (Njwaxu and Shackleton 2019). Our findings for bats somewhat contradict ecological suc-

cession theory that predicts an increase in both faunal and vegetation diversity through time (McIntosh 1981). Birds, for example, are a taxon which often display an increase in species richness and diversity as succession proceeds (Serong and Lill 2012; Dario 2017), but this appears to differ for bats, possibly on account of the commonality of generalist foraging guilds that are active in different parts of patchwork landscapes. It is also possible that 10-year time differences in field abandonment are too short to detect differences in insectivorous bat community structure, especially due to the high mobility of bats. Although tree species richness and diversity increase with time, trees in former field plots are much smaller in structure and these plots have much lower biomass (Shackleton et al. 2013; Njwaxu and Shackleton 2019); as such they do not yet provide forest habitat needed by specialist forest bat species and are inhabited by generalist and open-area foraging species.

By comparison, species richness in forest fragments was low, comprising only nine species from seven genera. Five of these species were clutter-edge, and four open-air foragers, with no clutter species recorded, despite the forest specialist *R. swinnyi* being present in the nearby forests of Silaka and Dwesa (Moir et al. 2020a). This lack of forest specialists may reflect the limited forest fragment sample size or the very small nature of these fragments in a larger patchwork landscape. Smaller forest fragments also have more pronounced edge effects which can reduce the suitability of the forest interior for specialists (Webala et al. 2019). It is unsurprising that both species and functional richness were lower in forest fragments than nearby intact forests, as forest specialists rarely persist in small fragments (Farneda et al. 2015). Functional evenness, by contrast, is relatively high in fragments, reflecting high bat activity along forest edges as insect abundance is typically supported by edge habitats (Heim et al. 2018); and bats use treelines as commuting corridors (Kalcounis-Rueppell et al. 2013). With the passage of time the increase in forest patch size through natural afforestation of former fields might promote the presence of rarer forest specialist species (Castro-Luna et al. 2007).

The five open-air foragers commonly recorded in former fields are classified as urban-exploiter species (Marsden et al. 2023), so they may be pre-adapted to landscapes inhabited and modified by humans. *Mops midas* was an unexpected occurrence and our records of it in this study represent a putative range extension for this species (Monadjem et al. 2020). The former fields, now predominantly comprising *Vachellia karoo* woodland, provide suitable habitat not only for clutter-edge species but for the clutter species, *R. acrotis*, as found in previous savanna-woodland studies (Csorba et al. 2003; Stoffberg et al. 2012). Fahr and Kalko (2011) found that West African savannas had similar and comparable bat diversity and species richness to nearby forest inlets.

Foord et al. (2018) found low bat species turnover between site localities within a matrix of settlements, agricultural fields, and rangeland in the Limpopo Province of South Africa, and concluded it was likely because bats perceived different land use types as one habitat for foraging and roosting. Heterogeneous landscapes and those with corridors (i.e. hedgerows) have been linked to an increase in insectivorous bat diversity and activity (Frey-Ehrenbold et al. 2013; Froidevaux et al. 2019; Rodriguez-San Pedro et al. 2019), and anthropogenically altered environments within a rural setting (buildings, roads, gardens) contribute to landscape heterogeneity. Our study found site proximity to roads positively influenced open-air species and *R. acrotis* presence. Roads have been shown to increase arthropod diversity and generate flyways for bats to commute between forest fragments and woodlands (Swart et al. 2019; Swartz et al. 2022). Elsewhere, roads have been seen to negatively affect bats,

increase call attenuation due to noise pollution (Finch et al. 2020) and to act as a barrier for movement (Laforge et al. 2021), although this may not apply here on account of the rural nature of our study site (with poor quality gravel roads and very low traffic volumes and light pollution). Conversely, our study found that proximity to buildings negatively affected the presence of the clutter forager *R. acrotis* and clutter-edge species presence, unlike previous studies that have found that clutter-edge species can adapt to utilising buildings and associated disturbances (Jung and Kalko 2010; Stone et al. 2015; Schoeman 2016). Other studies have found that light and noise pollution, associated with people and buildings, have been shown to negatively affect bat species richness and clutter-edge species presence (Stone et al. 2015; Schoeman 2016; Azam et al. 2016). Our study found that western facing slopes positively influenced bat species richness and diversity. These slopes may afford shelter from adverse weather conditions (Mucina and Rutherford 2006) such as wind, which has been shown to reduce bat foraging activity (Smith and McWilliams 2016).

Conclusions and recommendations

Contrary to our expectations, former fields within the Willowvale region have greater insectivorous bat species richness, Shannon-Weiner diversity, activity, and functional diversity than forest fragments. They also show similar species richness to, and greater functional diversity than, intact forests nearby, although the former fields lack the forest specialist species *R. swinnyi*. Forest specialist clutter foragers, particularly cave and crevice roosting bats, appear to be notably vulnerable to alternative forms of land-use (Clement et al. 2024). Both the high functional diversity of, and the similarity in species composition between former fields and nearby intact forests highlights the conservation potential associated with deagrarianization. This is particularly true in the Maputaland-Pondoland-Albany biodiversity hotspot along the eastern seaboard of South Africa, identified by Strassburg et al. (2020) as a target area in terms of increasing carbon sequestration and reducing biodiversity loss and extinction debt. The results of our study suggest former fields in the Eastern Cape, South Africa are diverse habitats, promoting high species richness and functional diversity of insectivorous bats and could contribute significantly to mitigating extinction debts. As such, we recommend that some of these former fields should be left to return to forest patches and which could be sped up or enhanced through active restoration programs, which would provide jobs locally and reduce poverty, while others should be allowed for community use, promoting more savanna-type landscapes. In terms of management, sustained follow-up clearing of the problematic invasive alien plant *L. camara* in former fields is also essential to ensuring long-term recovery of these sites and promoting the supply of ecosystem services and biodiversity preservation (Shackleton et al. 2013; Barahukwa et al. 2023). Although there was high bat biodiversity in former fields undergoing passive reforestation, we highlight that conserving large intact forests remains critically important in terms of conserving forest specialist species – not yet found in former fields.

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Data availability The data supporting the results reported in the manuscript are available in the supplementary material file.

Declarations

Competing interests The authors declare no competing interests.

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