



## Research Paper

# Bat guilds respond differently to habitat loss and fragmentation at different scales in macadamia orchards in South Africa

Sina M. Weier<sup>a,\*</sup>, Valerie M.G. Linden<sup>b,1</sup>, Antonia Hammer<sup>c</sup>, Ingo Grass<sup>d</sup>, Teja Tschardt<sup>e</sup>, Peter J. Taylor<sup>a,b</sup>

<sup>a</sup> Department of Zoology & Entomology & AfriMontane Research Unit, University of the Free State, QwaQwa Campus, Phuthaditjhaba, South Africa

<sup>b</sup> SARChI Chair on Biodiversity Value & Change & Core Team Member of the Centre for Invasion Biology, School of Mathematical & Natural Science, University of Venda, Thohoyandou, South Africa

<sup>c</sup> Zoological Institute and Museum, University of Greifswald, Greifswald, Germany

<sup>d</sup> Ecology of Tropical Agricultural Systems, University of Hohenheim, Stuttgart, Germany

<sup>e</sup> Agroecology, Department of Crop Sciences, University of Göttingen, Göttingen, Germany



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## ABSTRACT

Bats have been shown to provide successful pest suppression in different land-use systems globally. Recent research demonstrates high economic values of pest suppression by bats also in macadamia orchards, which is enhanced by natural habitat patches at orchard edges. We investigated the impact of the conversion of natural to agricultural (macadamia-dominated) habitats. Using ~65,000 recorded bat call sequences; we studied bat communities in three land use types: a nature reserve, macadamia orchards with and without adjacent natural habitat patches. All study sites are situated on the southern slopes of the Soutpansberg, northern South Africa. Species richness varied significantly between the nature reserve and the macadamia orchards, but did not between orchards with and without neighbouring natural habitat. Within the orchards, activity of edge space foraging (dependent on e.g. forest edges) bats was greater at natural edges, whereas open space aerial foraging species (hunting above canopy) were more active at human-modified edges. Although seven narrow space foraging (i.e. dense vegetation dependent) bat species were identified at both orchard and reserve, this foraging guild occurred more frequently in the nature reserve (2.9–4.1% of all call sequences) than in the orchards (0.5–2.9% of all call sequences). Narrow space foraging bats were thus largely excluded from simplified agricultural landscapes, in particular where natural edge habitats are missing, compared to our natural control. The current trend in conversion of natural habitat in favour of macadamia monocultures, especially if remnant natural patches at orchard boundaries are removed, will have widespread detrimental effects on bat diversity. The resulting reduced biological pest suppression by bats and increased reliance on chemical control may further exacerbate biodiversity declines.

## 1. Introduction

Bats provide a number of important ecosystem services and their role as biocontrol agents has been highlighted recently (e.g. Kunz et al., 2011; Ghanem and Voigt, 2012; Karp and Daily, 2014; López-Hoffman et al., 2014; Maas et al., 2016; Linden et al., 2019). Bats can have enormous economic importance through suppressing pest insects in agriculture (Cohen et al., 2020; Russo et al., 2018), and may reduce potential health risks by suppressing mosquitos and limiting the distribution of diseases like malaria (Ghanem and Voigt, 2012). Insectivorous

bats, therefore improve food security (Wanger et al., 2014), and are gaining even more importance in a society that is increasingly focusing on healthy and organic food (Puig-Montserrat et al., 2021).

Bat populations are globally declining due to multiple threats like habitat loss and fragmentation, hunting for bush meat, windfarms and the North American White-nose syndrome (Frick et al., 2016; Jones et al., 2003). Changes in habitats (e.g. due to intensified agriculture) are mostly anthropogenically mediated and predicted to continue and even increase over the next decades (Tilman et al., 2001). Generally, bats seem to prefer less intensive or organic agroecosystems with remnants of

\* Corresponding author.

E-mail address: [weier.sm@ufs.ac.za](mailto:weier.sm@ufs.ac.za) (S.M. Weier).

<sup>1</sup> These authors contributed equally to this work



**Fig. 1.** The map a) is showing the study area in Limpopo Province, South Africa (inset), the white boxes represent the study sites as illustrated in the photographs b) Luvhondo Private Nature Reserve and c) a natural orchard edge with macadamia orchards bordering natural vegetation (Orchards) and d) a human-modified edge with continuous macadamia plantings (Orchards). Map images courtesy of GoogleEarth and QGIS.

natural habitat over intensively managed agricultural systems (Kelly et al., 2016; Wickramasinghe et al., 2003; Wordley et al., 2017).

Linden et al. (2019) found that biocontrol by bats (and birds) in South African macadamia orchards is higher at natural orchard edges and their exclusion from macadamia trees is associated with a 30% yield loss. Similarly, Kolkert et al. (2021) found that predation pressure by both birds and bats was sometimes greater at cotton crop edges but that this depended on the time of year and crop cover. Natural vegetation on farms provides roost sites but also aids with orientation and bats often use natural corridors and forest edges as flight paths. Woodlands and alleys of trees can increase bat activity in an agricultural landscape (Kalda et al., 2015). By contrast, monocultures could potentially limit bat dispersion range, especially in the case of sensitive species (Pinaud et al., 2018). In general, this means that the structural simplification of orchards may compromise the pest suppression services of some bat species (Costa et al., 2019).

Bat species respond differently to the same landscape matrix and show varying levels of sensitivity to habitat destruction, light pollution and other human-induced stressors (Frey-Ehrenbold et al., 2013; Mtsetfwa et al., 2018; Rowse et al., 2016; Russo and Ancillotto, 2015; Shapiro et al., 2019). This varying response is related to their foraging ecology, where three general foraging guilds can be recognised. Bats that depend on vegetation (narrow space foraging bat species) are

known to be especially sensitive (Cooper-Bohannon et al., 2016; Denzinger and Schnitzler, 2013; Frey-Ehrenbold et al., 2013; Monadjem et al., 2020). The removal of natural vegetation can have significant impacts on these bats, as they rely on closed vegetation structures for feeding and navigation. Edge space foraging species likewise depend on forest edges or linear landscape features (Monadjem et al., 2020). Open space aerial foraging bat species, on the other hand, are known to be more tolerant to human disturbances. Some open aerial species are reported to hunt under street lights (Rowse et al., 2016), roost in houses and they seem possibly less affected by changes in vegetation, as they generally hunt in mid-air, above the canopy (Jung and Threlfall, 2016). Mtsetfwa et al. (2018) found these different activity patterns to be present in a southern African monocultural landscape, with clutter-feeding species being almost absent, while the activity of open-air feeding species increased relative to other guilds. When looking at ecosystem services within an agricultural landscape, it is hence of great importance to fully understand the driving forces behind bat community compositions, activity patterns and behaviour.

Insectivorous bats are relatively abundant in South African macadamia orchards and this high activity is suggested to be positively linked to (semi-) natural vegetation as well as pest insect (Hemiptera) abundances (Taylor et al., 2013a; Weier et al., 2018). The South African macadamia industry is rapidly expanding (SAMAC, 2019) and the

ongoing conversion of natural vegetation to macadamia orchards could therefore negatively affect bat diversity, activity and associated biological pest suppression services.

Our study focuses on the effect of natural habitat loss on bat communities comparing different habitat types; natural areas ('Soutpansberg Mountain Bushveld'), and macadamia orchard edges with natural habitat patches ('Soutpansberg Mountain Bushveld' and 'Tzaneen Sour Bushveld'; see Section 2.1 Study area), and without natural habitat patches (human-modified edges), in the same southern African region, the Soutpansberg Mountain Range (Mucina and Rutherford, 2006).

We hypothesised bat richness, diversity and activity to be higher in the natural areas compared with the macadamia-growing area, and this to be particularly true for sensitive or specialised narrow space foraging species. Within the macadamia-growing area, we predicted a similar trend with higher diversity and activity at natural versus human-modified orchard edges.

## 2. Methods

### 2.1. Study area

This study took place in Soutpansberg Mountain range of South Africa's northernmost province, Limpopo, which borders on Botswana, Zimbabwe, and Mozambique. The Soutpansberg is part of the UNESCO Vhembe Biosphere Reserve and known as a Centre for Plant Endemism (UNESCO, 2010). Furthermore, animal diversity is remarkably high: the area harbours about 75% of South Africa's bird species and 60% of South Africa's mammal species (Van Wyk and Smith, 2001; UNESCO, 2010). The Soutpansberg is also a bat richness hotspot in South Africa (Taylor et al., 2013b). The climate in this geographical region can be divided into a dry (winter) and a wet (summer) season, with the main rainfall between November and April. Orographic mist and rainfall are reported to play an important role on the southern Soutpansberg slopes, whereas the northern slopes experience a rain-shadow effect, which results in lower precipitation (Mostert et al., 2008).

Sampling of the macadamia orchards took place in Levubu, one of South Africa's largest and oldest macadamia growing areas over two macadamia growing seasons (from September 2015 to March 2017). Levubu is situated on the southern slopes of the Soutpansberg mountain range. Due to its subtropical climate and high annual precipitation (average of over 900 mm) this area is very productive and other major crops planted here are; banana (Zingiberales: Musaceae), avocado (*Persea*), timber (*Eucalyptus*) and to a lesser extent mango (*Mangifera*), pecan (*Carya*), lychee (*Litchi*) or maize (*Zea*). To compare macadamia orchards with and without natural habitat patches, we selected six macadamia orchards, situated at 700–900 m above sea level and therefore similar in abiotic conditions. The orchards are situated between the towns of Thohoyandou (22°59'03.7S, 30°27'12.8 E) and Louis Trichardt (23°03'03.6S, 29°55'12.7 E). Each farm had remnants of natural vegetation bordering their macadamia orchards. We selected two sites on each farm with the same macadamia varieties and similarly aged trees, one bordering stretches of natural vegetation (natural edge) and one with continuous crops (human-modified edge). Sites with natural edge habitat (Fig. 1) consisted of macadamia orchards next to patches of natural woodlands of up to 20 ha in size and about 100–200 m wide. All but one of these patches are connected to further patches of natural vegetation. Mucina and Rutherford (2006) classified the natural vegetation in this area as 'Soutpansberg Mountain Bushveld' and 'Tzaneen Sour Bushveld'. Human-modified edges (Fig. 1b) consisted of orchards surrounded by more macadamia plantings, in some cases crossed by farm roads and situated at a distance of 160–530 m to the next natural vegetation patch (Fig. 1c).

In summary, to investigate differences between the natural areas and macadamia orchards, we sampled a total of six different sites in the Luvhondo Private Nature Reserve and nine sites at natural edge habitats in macadamia orchards in Levubu, in November and December 2019.

The nine sites in the orchards were different sites than those selected in the first part of the study, which took place at the foothills of the Soutpansberg. In order to compare the Nature Reserve and the orchards directly we chose a wider range of altitudes in order to have similar abiotic variations. Sampling sites in Levubu are situated at 700–900 m, 1200 m and 1300 m above sea level; sampling in the nature reserve took place at 1100 m, 1200 m and 1300 m (a.s.l.). The Luvhondo Private Nature Reserve is located about 70 km linear distance from the macadamia orchards also on the southern slope of the Soutpansberg (Fig. 1). The area is about 5000 ha in size and was proclaimed a nature reserve in 2014, which excludes agricultural land use as well as other activities such as hunting and bush clearing. The vegetation in this area has been classified as 'Soutpansberg Mountain Bushveld', which includes the 'Northern Mistbelt Forest' (Mucina and Rutherford, 2006). Both, habitat types the 'Soutpansberg Mountain Bushveld' and the 'Tzaneen Sour Bushveld' are part of the sub-tropical savannah biome and comprise densely treed thickets, especially because of the absence of browsing species in the study area (Hahn, 2017).

### 2.2. Data collection

Acoustic data were collected at different times for the within orchard comparison and the comparison of the orchards and the natural areas, using SM BATS2+ and SM4BAT-FS bat detectors respectively, as outlined below.

We used passive acoustic monitoring to assess the influence of orchard edges on bat activity and diversity in a paired design over two macadamia growing seasons. We surveyed one natural as well as one human-modified habitat edge per farm, resulting in 12 sites. With six stationary bat detectors (Song Metre BAT2+, Wildlife Acoustics Inc., USA), we recorded for 12 h from sunset to sunrise over two consecutive nights per month. We sampled monthly in the first season (September 2015 until August 2016) and in the second season only every three months, starting with August 2016 until the end of the season in March 2017. We sampled each site for 14 months over two nights per month, adding up to a total 336 detector-nights. Due to technical faults and incomplete samples, we had to reduce the sample size to 265 detector-nights. For each night we also recorded the moon phase and average temperature.

To assess differences in insectivorous bat activity, diversity and species richness between a more natural land use type (the nature reserve) and the intensively managed macadamia orchards we again used passive acoustic monitoring with stationary SM4BAT-FS bat detectors (Wildlife Acoustics Inc., USA). We recorded twice for two consecutive nights at the six sites in the nature reserve in November and December 2019 and at nine sites for two consecutive nights in the macadamia orchards in November 2019. Due to accessibility and logistical issues, we could not repeat the December sampling in the Nature Reserve. Again, we recorded the average temperature and moon phase for each site as well as the altitude and the date of the first rain for that season.

We sampled a total of 48 detector-nights in the nature reserve. Due to technical failure, we used 47 nights for the final analysis. Furthermore, we recorded a total of 18 detector-nights in the macadamia orchards.

Microphones were always erected on 4 m high flagpoles at an angle of approximately 45° and the bat detectors were moved randomly between sites. Recordings took place on dry nights only due to logistical constraints.

### 2.3. Data analysis

We identified all call sequences manually to species level using AnaloookW (version 3.8; Corben, 2006) after converting them to zero-crossing (ZC) files with Kaleidoscope (version 1.1.15; Wildlife Acoustics, Inc., USA). We used frequencies (minimum, maximum, characteristic, mean and frequency of the knee), duration and slope of

each call sequence to assign recordings to a certain species according to reference libraries of Southern Africa (Monadjem et al., 2020; Taylor et al., 2013b; Table A.1). Recordings that we could not assign to a species with confidence were labelled “Unknown” and excluded from further analysis. Repeatedly occurring call sequences with distinct characteristics, which could not be confidently assigned a species were labelled accordingly as ‘potential species’ (e.g. “Vesper58”). However, throughout the study, the three *Myotis* species (*M. bocagii*, *M. tricolor*, *M. welwitschii*) were grouped and treated as one, due to largely overlapping call parameters and few available reference call sequences.

In addition to AnalookW, we used the programme Batexplorer (Version 2.1; Elekon AG, Switzerland) to support bat call analysis when AnalookW showed indistinct results.

No automated call analysis was used due to the high amount of overlap in bat call parameters in some of the recorded species (Taylor et al., 2013b; Rydell et al., 2017). Each bat species was furthermore assigned to a foraging guild as being either “Narrow space forager”, “Edge space forager/Clutter-edge feeder” or “Open space aerial forager” (Denzinger and Schnitzler, 2013).

Identified bat call sequences were converted into Miller’s activity index (Miller, 2001), accounting for species specific activity patterns and other biases in recording (e.g., proximity to roosts) and counting the number of active minutes per species rather than the number of bat passes. We furthermore used the packages “iNext” v. 2.0.17 (Hsieh et al., 2018) and “ggplot2” v. 2.2.1 (Wickham, 2016) in R v. 3.5 (R Foundation for Statistical Computing, Vienna, Austria) to do an incidence-based rarefaction approach measure to assess sampling sufficiency.

### 2.3.1. Comparison of natural and human-modified orchard edges

We divided the months of recording into high (December until and including May) and low (June until and including November) season. Macadamia fruit development takes place during the high season during which the pest insect pressure increases. The high season furthermore coincides with the wet/rainy season in the study area.

Generalized linear mixed models (GLMM) were used to assess differences in bat activity patterns per night, using the sum of active minutes (Miller’s Index). Due to overdispersion of the count data we used the “lmer” function with a log transformation. The global model included edge type, season, feeding guild, moon phase and temperature as explaining variables with year, month and farm as random factors. The “dredge” function from the “MuMIn” package v. 1.40.0 (Barton, 2017) was used for the final model selection based on Akaike’s Information Criterion, resulting in a final model with edge, season and feeding guild (Table 3). All analyses were done using R v. 3.5 and packages “lme4” version 1.1-14 (Bates et al., 2015), “multcomp” version 1.4-7 (Hothorn et al., 2008).

We furthermore related the activity levels of most dominant species to outcomes of an earlier experimental exclusion study in the same macadamia orchards and landscape settings (Linden et al., 2019).

### 2.3.2. Comparison of the different land use types

The bat activity per foraging guild and altitude (Miller’s Index) as well as species richness and diversity were analysed and compared between the nature reserve and the macadamia orchards. To prevent bias from differences in number of sampling nights, we calculated the average number of call sequences for the nature reserve (47 detector-nights) and the macadamia orchards (18 detector-nights) for direct comparisons.

EstimateS (version 9.1; Colwell, 2013) was used to calculate species richness (expected number of species) and species diversity (inverse Simpson’s) indices using a sampling-based incidence data approach for multiple sets of replicated sampling units. We used the packages ‘stat’ and ‘lme4’ (Bates et al., 2015) to fit linear models (lm) testing the relationship between species richness and diversity with the variables altitude and region (nature reserve or macadamias). After checking for normal distribution (Shapiro-Wilk test), a generalized linear model with

a ‘poisson’ distribution was fitted to test the response of the species richness indices.

To assess the relationship between total bat activity as well each individual foraging guild and the variables altitude, temperature, first rain, region and moon phase, generalized linear mixed models (GLMM) were applied using the package ‘lme4’ (Bates et al., 2015). The models were tested for normality (Shapiro-Wilk test) and models with non-normally distributed data were applied using a ‘Poisson distribution. Furthermore, we used the package ‘performance’ (Lüdtke et al., 2020) to check for overdispersion and multicollinearity of data. Whenever, overdispersion was detected, models were fitted using a negative binomial distribution. Again, the “dredge” function based on Akaike’s Information Criterion was used for the final model selection. The variable ‘site’ was used as a random factor to account for pseudo replication (various sampling nights per sampling site) whereas the variables temperature, moon phase, altitude, region and first rain (i.e. sampling before or after first heavy summer rainfalls) were treated as fixed effects. The variables temperature, altitude and moon phase were furthermore scaled.

## 3. Results

Between 2015 and 2017, the passive monitoring and conversion to Miller’s activity index resulted in a total of 43,394 active minutes recorded over 265 nights. We identified a total of 25 species. In 2019, during 47 sampling nights in the nature reserve, we recorded a total of 15,981 active minutes. In 2019 in the macadamia orchards, a total of 1838 active minutes were recorded during 18 sampling nights. Furthermore, based on rarefaction we estimated a total of 31 bat species in the nature reserve and 29 bat species in the macadamia orchards (Table A.1).

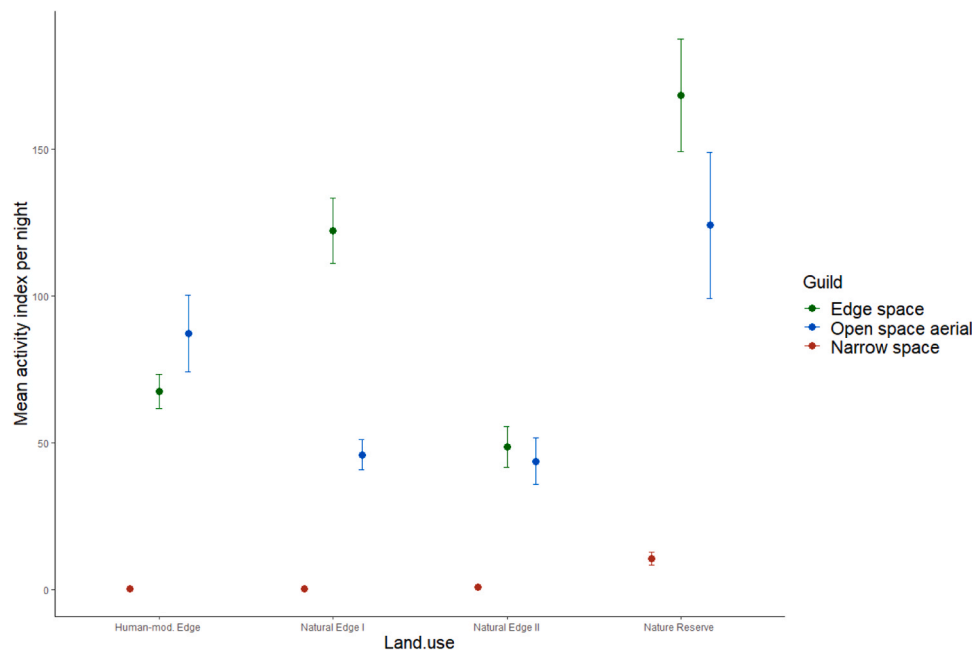
### 3.1. Activity, diversity and community composition at the different orchard edges

Edge space and open space aerial foraging bat species were generally more active than narrow space foraging bats at both edges (Table 1; Fig. 2). The most dominant species overall were three Edge space and two open space aerial foraging species (Table 2). Total bat activity was almost equal between the two orchard edges, but we observed differences when looking at guild and species level. At the human-modified edge, activity of open space aerial foraging species was higher than at the natural orchard edge or compared to the other foraging guilds. The two most dominant species at this edge were edge space foraging bat species. Their call sequences accounted for approximately 40% of all call sequences at the human-modified edge, while the open space aerial foraging guild accounted for about 56% of the call sequences. The Edge

**Table 1**

Model results from the macadamia orchard edge-types part of the study (see Methods). Bat activity index (AI), summed per night in response to edge type (natural and human-modified), season (wet and dry) and foraging guild (narrow space, edge space and open space aerial foragers).

	Estimate	SE	Z	P
Fitted model: AI (log + 1) ~ Edge * Season * Guild + (1 Farm) + (1 Month)				
Intercept	0.19	0.21	0.93	0.354
Natural edge	-0.05	0.16	-0.35	0.728
Dry Season	-0.16	0.21	-0.75	0.454
Edge guild	3.81	0.15	24.74	<0.001
Open aerial guild	3.76	0.15	24.42	<0.001
Natural Edge: Dry Season	0.12	0.26	0.45	0.652
Nat. edge: Edge guild	0.57	0.22	2.61	0.009
Nat. edge: Open aerial guild	-0.38	0.22	-1.73	0.084
Dry season: Edge guild	-0.76	0.26	-2.89	0.004
Dry season: Open aerial guild	-1.22	0.26	-4.65	<0.001
Nat. edge: Dry: Narrow guild	0.08	0.36	0.23	0.817
Nat. edge: Dry: Open aerial guild	-0.22	0.36	-0.59	0.554



**Fig. 2.** Bat activity showing mean ( $\pm$ SE) active minutes for each foraging guild (narrow space, open space aerial and edge space foraging guild) at either natural and human-modified orchard edges for sampling period 2015–2017 as well as at the natural orchard edges and the Luvhondo Private Nature Reserve for the sampling period of 2019.

**Table 2**

Model parameters (i.e. estimate values, standard error (SE),  $z$ - and  $p$ - values) for the final models from the comparison between a nature reserve and macadamia orchards (see Methods), testing the effects of several variables on total bat activity and foraging guild activity (Miller's index), respectively; AICc values for the global models and for the final models (bold) are shown; the significance level is  $p < 0.05$ .

	Estimate	SE	$z$	Pr ( $>  z $ )	AICc
<b>Total activity</b>					<b>816.9/815.2</b>
Intercept	5.50	0.17	32.27	<0.001	
Temperature (scale)	0.31	0.08	3.83	<0.001	
Region	-1.42	0.24	-5.76	<0.001	
First rain	0.44	0.16	2.69	0.007	
<b>Narrow space guild activity</b>					<b>366.9/357.3</b>
Intercept	2.02	0.40	4.99	<0.001	
Region	-2.60	0.64	-4.03	<0.001	
<b>Edge space guild activity</b>					<b>716.8/711.1</b>
Intercept	4.93	0.21	23.15	<0.001	
Region	-1.27	0.29	-4.32	<0.001	
Temperature (scale)	0.44	0.07	6.10	<0.001	
<b>Open space aerial guild activity</b>					<b>708.8/704.8</b>
Intercept	3.92	0.28	13.91	<0.001	
Region	-1.65	0.40	-4.10	<0.001	
First rain	1.29	0.26	4.93	<0.001	
Moon (scale)	-0.25	0.11	-2.33	0.019	

space forager activity was higher at natural edges, while open space aerial activity was lower here. Most dominant bat species at the natural edge were three edge space foragers. These three species accounted for 51% of all call sequences at the natural edge and all edge space species made up about 72% of all call sequences here. Edge space foraging bat species only accounted for about 43% of all call sequences at the human-modified edge. All feeding guilds were less active during the low (winter/dry) season compared to the high (summer/wet) season. The final model explained about 73% of the variation ( $R^2 = 0.73$ ), whereas moon phase and temperature were not included, but only edge type, season and feeding guild with interactions.

The rarefaction analysis showed that we can assume a complete

sampling effort (likely no further species to be added by additional recording nights at the sampling sites) with an estimated species richness of 21, which did not differ between seasons or between natural and human-modified edges (Fig. A.1). Likewise, there were no differences in Shannon as well as Simpson diversity during the wet season for either edge, while the Simpson's concentration index generally showed slightly lower species diversity than the Shannon's entropy index. In the wet season, however, both edge settings showed lower species diversity than in the high season (Fig. A.1). Species diversity was lowest in the human-modified edge setting during the dry season.

### 3.2. Activity, diversity and community composition in the different land use types

The narrow space foraging guild was the rarest feeding guild at all altitudes and in both study areas. However, this foraging guild occurred more frequently in the nature reserve than in the orchards. The percentage share of narrow space foragers of the overall foraging guild activity index was 3.25% (1100 m), 4.14% (1200 m) and 2.95% (1300 m) in the nature reserve and 0.66% (700–900 m), 2.9% (1200 m) and 0.59% (1300 m) in the macadamia orchards (Fig. 2). The other two foraging guilds, the open space aerial and the edge space foragers, appeared noticeably more frequent than narrow space foragers in both regions and at all altitudes.

#### 3.2.1. Guild-specific activity responses

Region (nature reserve or macadamia orchards), temperature, and the occurrence of first heavy rainfalls of the wet summer season clearly had a significant effect on total bat activity (Table 2).

The number of bat call sequences in the macadamia orchards was significantly lower than in the nature reserve. Furthermore, bat activity increased significantly with temperature and was significantly lower after the first heavy rainfalls.

Region was the only variable retained in the final model testing the activity of the narrow space foraging guild and had a significant impact on their activity (Table 2). The activity of narrow space species was significantly higher in the nature reserve than in the macadamia orchards.

**Table 3**

Model parameters testing the effects of altitude and region on species diversity (inverse Simpson's diversity index) and species richness (expected number of species); the significance level is  $p < 0.05$ .

Species diversity	Estimate	SE	t value	Pr (> t )
Intercept	27.444	4.022	6.824	<0.001
Altitude	-0.004	0.003	-1.126	0.282
Region	-7.059	1.453	-4.857	<0.001
Species richness	Estimate	SE	z value	Pr(> z )
Intercept	3.541	0.372	9.513	<0.001
Altitude	<0.001	<0.001	-0.638	0.523
Region	-0.445	0.128	-3.490	<0.001

The variables region and temperature also had a significant impact on the narrow space foragers activity (Table 1). We recorded a significantly higher number of those species in the nature reserve than in the macadamia orchards and with increasing temperature, their activity increased significantly.

The activity of the open space aerial foraging guild was influenced by moon phase, first rain and region (Table 2). Their activity was again significantly higher in the nature reserve than in the macadamia orchards and decreased significantly with increasing moon phase and after the first heavy rainfalls. The only variable retained in all final models (total activity and activity of each foraging guild) was the variable region. The nature reserve consistently showed a significantly higher bat activity than the macadamia orchards.

### 3.2.2. Diversity estimates

Both species diversity and richness were significantly higher in the nature reserve than in the macadamia orchards, whereas altitude had no significant effect (Table 3).

Rarefaction analysis based on incidence data for 47 sampling nights in the nature reserve showed a complete sampling effort and an estimated species richness of 31 bat species, while Shannon's entropy index and inverse Simpson's diversity index were lower, indicating a species diversity of 27 and 25 species (Fig. A.2). For the 18 sampling nights in the macadamia orchards, rarefaction analysis again showed a complete sampling effort, however with broader confidence intervals, and an estimated species richness of 29 bat species, a Shannon's entropy index of 23 species and an inverse of Simpson's diversity index of about 21 species.

## 4. Discussion

We compared different habitat types, natural areas and commercial macadamia orchards with and without natural vegetation edges, to investigate the importance of natural landscapes and natural vegetation patches to bat communities. We demonstrated guild specific edge preferences in bat communities in macadamia orchards that varied with season and were likely linked to greater macadamia pest suppression services close to natural edges (Linden et al., 2019). Edge space species were identified to rely on natural orchard edges, while open aerial space foraging bat species preferred the human-modified edges. Species richness, diversity and activity were significantly higher in the nature reserve than in the macadamia orchards. The bat community composition and activity clearly showed a near exclusion of narrow space foraging bat species from the monoculture-dominated, simplified macadamia landscapes.

### 4.1. Species richness and functional composition

Our observed species richness of 25–29 species in local macadamia orchards, is higher than that of previous studies (up to 22 species), but in line with estimates of local species richness from other studies in

southern Africa (Cooper-Bohannon, 2016; Linden et al., 2014; Monadjem et al., 2020; Taylor et al., 2013a, 2013b; Weier et al., 2016, 2018). Our results indicate that an intensively farmed agricultural landscape is still able to support high bat species richness, possibly also due to the nature of macadamia orchards, as suggested by Kalda et al. (2015), who found that bats prefer alley-like tree plantings as a second option after woodlands. Apart from being a landmark suitable for orientation and connectivity, alleys likely also provide more of an 'overstorey' than single tree lines.

Comparing the community composition and activity in macadamia orchards to the nearby nature reserve, however, we found that narrow space foraging species were almost absent from the macadamia landscape. The narrow space guild occurred noticeably less frequently than the other guilds, but still more frequently in the nature reserve than in the macadamia orchards. Furthermore, there was significantly more bat activity (total and feeding guild) in the nature reserve than in the macadamia orchards. Species diversity and species richness were also significantly higher in the nature reserve. Our results suggests that the sensitive narrow space foraging species have already been nearly excluded from the intensively farmed macadamia landscape. Similar results from studies in intensive agricultural systems such as sugarcane monoculture, which found a near absence of narrow space foraging species (Heim et al., 2015; Toffoli and Rughetti, 2017; Mtsetfwa et al., 2018) support our findings. Aside from the preference of this guild for dense, cluttered vegetation, their absence could also be due to farm management practices. A study in Britain comparing bat activity on organic farms to that on conventional farms has reported that narrow space foraging *Rhinolophus* (horseshoe bat) species are only active on organic farms (Wickramasinghe et al., 2003). Macadamia orchards are extensively sprayed with pesticides, which may deter sensitive species like the Rhinolophidae (Bontadina et al., 2000; Jan et al., 2020). Additionally the findings of Costa et al. (2019), showed that bat activity patterns are affected by structural simplification. In highly transformed rural settlements and croplands directly east of the Levubu study area, *Rhinolophus* species are completely absent (Foord et al., 2018).

### 4.2. Guild specific activity and impacts for biocontrol

While total bat activity was not affected by the orchard edges, edge space foraging species were more active at natural edges and open space aerial foraging species more active at human-modified edges. Pest suppression services by bats and birds were previously found to be higher at these natural edges, compared to human-modified edges (Linden et al., 2019). Edge space foraging bat species may thus potentially contribute more to these biocontrol effects on crop yield and quality, but could be facing similar activity declines to narrow space foraging bat species, with the ongoing removal of natural vegetation to create more croplands. In South Africa, this is at present particularly prevalent in the lucrative South African macadamia industry, with 6300 ha of new macadamia planted in South Africa in 2018 alone (SAMAC, 2019) often at the expense of natural habitat. This can result in widespread landscape homogenisation, which severely threatens bat diversity and their ecosystem services. Our regional comparison supports this prediction showing significant differences in total bat activity (and feeding guild activity, respectively) between the nature reserve and the macadamia orchards. Decreased biocontrol through pest suppression may in turn result in an increased need for chemical control and pesticide applications, which would result in an increase in production costs, as well as further pressure on remaining ecosystem services for example by predatory arthropods.

Previous studies in Europe suggest the importance of connectivity and heterogeneity in an agricultural landscape to conserve bat species richness, diversity and activity (Ancillotto et al., 2017, 2021; Frey-Ehrenbold et al., 2013; Kalda et al., 2015), especially for narrow

space foraging greater horseshoe bats (*Rhinolophus ferrumequinum*; Pinaud et al., 2018). However, even open-air feeders, which can be found to exploit monocultures such as southern African sugarcane plantations as foraging grounds, can be affected by the loss of roost sites or alternative prey species abundances (Shapiro et al., 2019). Agricultural monocultures can also cause loss of functional diversity, for example, specialised insectivores are absent from bird communities in cocoa plantations in Cameroon (Jarrett et al., in press).

Lower levels of activity for both edge space and open space aerial foraging guilds in the dry season can be explained by lower prey availability and pest insect abundances (Taylor et al., 2013a; Weier et al., 2018), but may also be due to colder temperatures in winter (Monadjem et al., 2020; Parker and Bernard, 2018). We cannot confirm observations of Shapiro et al. (2019), who found a seasonal dependence of narrow space foraging bats on sugarcane, which could possibly be explained by water availability. Since our study area is within a particularly high rainfall area with the mountain range providing many perennial streams, the artificial water bodies on farmland might be less of an attraction to local bats.

## 5. Conclusions

In principle, heterogeneous agricultural landscapes can support a high bat biodiversity, in particular if they are located close to natural areas such as nature reserves, as seen for our studied landscape in South Africa. However, under current levels of land-use change, these agricultural landscapes are increasingly homogenised by growing crop monocultures at the expense of natural habitat (Foley et al., 2005; SAMAC, 2019; Tilman et al., 2001; Tschardt et al., 2012).

Specialist species, like the horseshoe bats, have already been near excluded and their services lost, but even generalists are likely to be threatened if food resources and roosting sites become scarce. In turn, ecosystem services like pest suppression may become likewise highly threatened. Biodiversity loss and agricultural intensification are threatening the sustainability of crop production.

**Table A.1**

Summary of call parameters for all recorded bat species obtained from ANABAT recordings excluding ‘potential species’ (see Methods). N refers to the number of total call sequences used for these statistics and (n) to the number of individuals or recording sequences.

		Dur	Fmax (kHz)	Fmin (kHz)	Fk (kHz)	Fc (kHz)	Slope	N (n)
<b>VESPERTILIONIDAE</b>								
<i>Eptesicus hottentotus</i>	Mean	4.46	53.81	30.93	34.73	32.18	326.44	99 (9)
	SD	1.75	10.93	5.14	2.32	1.83	1214.91	
<i>Kerivoula argentata</i>	Mean	1.98	159.23	135.12	142.39	140.26	46.99	35 (11)
	SD	1.33	6.03	15.89	7.02	16.47	7660.20	
<i>Laephotis botswanae</i>	Mean	4.92	45.58	30.24	33.66	30.73	309.65	99 (6)
	SD	1.98	10.03	1.16	1.14	1.21	145.86	
<i>Myotis bocagii</i>	Mean	2.76	56.97	27.67	43.99	40.53	124.20	99 (8)
	SD	0.51	7.52	3.64	7.41	6.86	3364.36	
<i>Myotis tricolor</i>	Mean	2.75	62.29	29.13	56.04	51.92	468.23	45 (12)
	SD	0.70	7.35	3.03	7.82	7.66	440.50	
<i>Myotis welwitschii</i>	Mean	2.58	58.88	30.30	51.03	47.27	493.64	36 (11)
	SD	0.42	4.53	3.49	4.84	4.98	133.78	
<i>Neoromicia capensis</i>	Mean	2.47	50.69	33.67	39.85	35.90	-864.75	99 (9)
	SD	0.56	4.25	6.67	1.03	1.34	7241.84	
<i>Neoromicia nana</i>	Mean	301.04	149.97	77.16	1.00	3.17	68.52	99 (11)
	SD	214.60	85.61	6.86	0.48	0.80	2.18	
<i>Nycticeinops schlieffeni</i>	Mean	3.98	50.27	40.20	42.86	41.61	-708.66	104 (7)
	SD	2.13	9.84	5.93	0.75	1.35	5655.95	
<i>Neoromicia zuluensis</i>	Mean	3.74	61.20	46.65	49.86	48.41	-238.88	99 (9)
	SD	1.50	8.60	5.20	2.26	1.76	3564.48	
<i>Scotophilus dinganii</i>	Mean	3.52	47.09	31.86	36.27	33.43	363.33	99 (10)
	SD	2.09	7.53	6.25	1.63	1.26	166.43	
<i>Pipistrellus hesperidus</i>	Mean	5.03	52.59	44.75	46.89	45.46	21.95	99 (4)
	SD	1.75	4.32	3.24	1.16	1.05	2040.74	
<i>Pipistrellus rusticus</i>	Mean	3.68	62.19	51.22	55.52	53.50	-684.82	99 (20)
	SD	1.41	7.23	9.07	1.33	1.22	5904.04	
		<b>Dur</b>	<b>Fmax (kHz)</b>	<b>Fmin (kHz)</b>	<b>Fk (kHz)</b>	<b>Fc (kHz)</b>	<b>Slope</b>	<b>N (n)</b>
<b>MINIOPTERIDAE</b>								

(continued on next page)

Our results highlight the importance of a heterogeneous landscape in and around macadamia orchards, which provides connectivity, foraging and roosting sites through natural and semi-natural edge vegetation and corridors to promote the diversity of bat species and their ecosystem service provision.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendices

See Appendix Table A1 and Fig. A.1, Fig. A.2

Table A.1 (continued)

		Dur	Fmax (kHz)	Fmin (kHz)	Fk (kHz)	Fc (kHz)	Slope	N (n)
<i>Miniopterus natalensis</i>	Mean	4.08	61.46	52.27	55.55	54.08	-508.55	96 (11)
	SD	1.61	7.55	5.90	0.81	0.98	3897.77	
MOLOSSIDAE								
<i>Chaerophon ansorgei</i>	Mean	7.80	22.28	20.28	21.79	20.90	-226.44	99 (10)
	SD	3.63	1.52	3.04	1.19	0.99	1751.57	
<i>Chaerophon pumilus</i>	Mean	7.42	39.45	26.00	30.63	27.92	-357.75	99 (6)
	SD	4.04	8.59	5.24	2.69	2.46	2923.00	
<i>Mops condylurus</i>	Mean	3.88	34.50	27.89	31.59	29.03	-480.97	99 (12)
	SD	1.71	4.44	3.95	3.22	2.80	2206.86	
<i>Mops midas</i>	Mean	5.67	18.69	17.09	18.39	17.49	-120.48	99 (20)
	SD	3.18	0.81	2.01	0.66	0.67	998.33	
<i>Otomops martiensseni</i>	Mean	9.13	12.88	11.83	12.67	12.01	-31.73	99 (9)
	SD	5.96	1.09	1.40	0.98	0.83	563.48	
<i>Sauromys petrophilus</i>	Mean	6.35	41.46	29.31	31.89	29.85	117.33	103 (5)
	SD	2.42	6.35	2.95	3.62	1.74	1045.12	
<i>Tadarida aegyptiaca</i>	Mean	6.49	26.82	23.40	25.19	23.52	92.93	99 (8)
	SD	2.74	2.55	0.89	1.28	0.97	90.54	
EMBALLANURIDAE								
<i>Taphozous mauritanus</i>	Mean	5.71	28.35	22.97	27.43	26.05	-215.69	99 (14)
	SD	3.76	2.05	6.79	1.74	1.61	1248.24	
RHINOLOPHIDAE								
<i>Rhinolophus blasii</i>	Mean	12.22	89.17	84.55	87.25	87.92	31.81	7 (1)
<i>Rhinolophus clivosus</i>	Mean	13.58	91.66	85.46	90.21	90.28	-1708.34	31 (6)
	SD	12.83	1.12	13.29	1.52	1.74	10,903.27	
<i>Rhinolophus dartingi</i>	Mean	37.63	91.04	78.67	89.02	90.15	-222.94	8 (1)
<i>Rhinolophus rhodesiae</i>	Mean	36.75	105.41	82.04	102.95	102.76	-3258.50	27 (7)
	SD	29.39	5.74	34.64	5.65	5.62	12,326.04	
<i>Rhinolophus simulator</i>	Mean	13.54	79.65	67.51	78.73	78.77	-5663.39	69 (10)
	SD	13.02	8.63	23.43	9.07	9.37	16,360.82	
<i>Rhinolophus smitherii</i>	Mean	16.36	47.26	39.78	46.45	46.34	-195.04	65 (3)
	SD	11.26	5.09	14.96	5.57	5.66	1520.38	
HIPPOSIDERIDAE								
<i>Hipposideros caffer</i>	Mean	2.26	155.64	146.03	153.78	151.15	-1522.71	50 (6)
	SD	3.24	10.30	27.97	11.95	10.77	23,168.41	

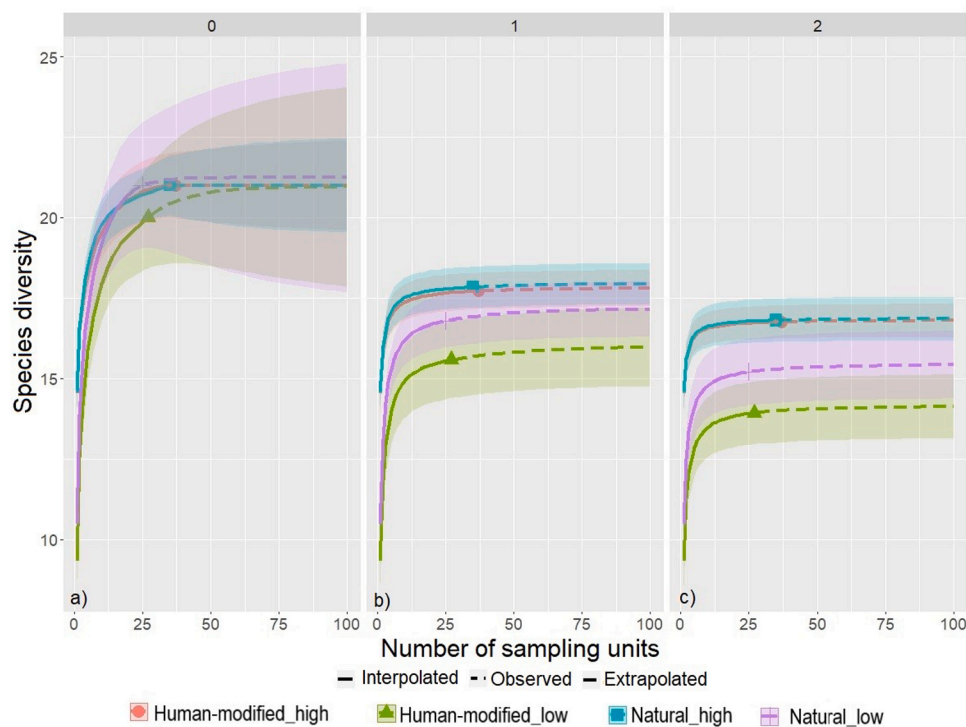
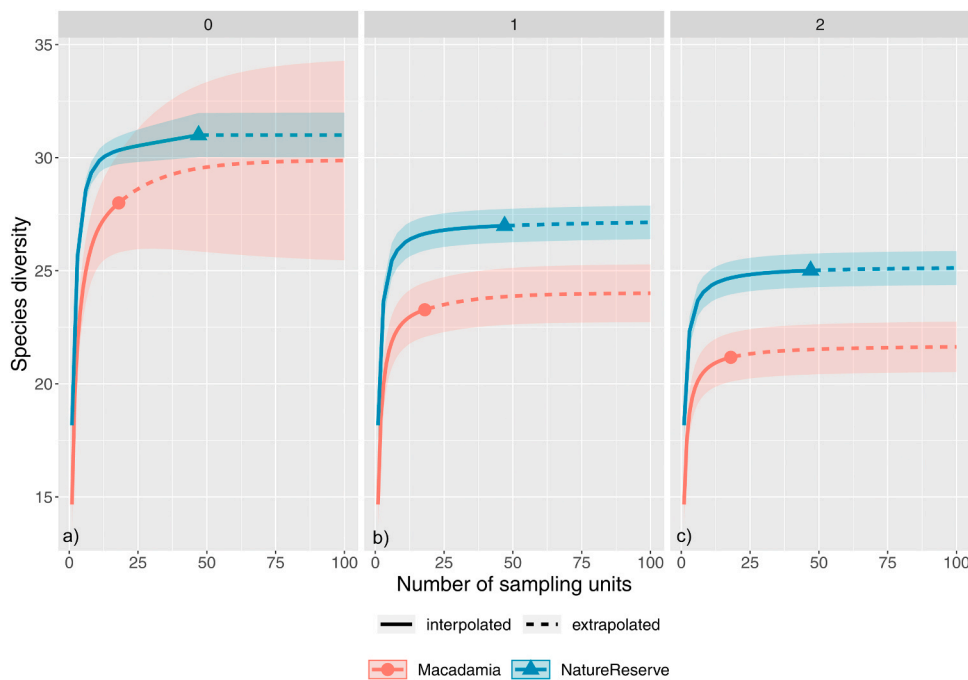


Fig. A.1. Incidence based diversity estimates with respect to sample coverage (Hill numbers) for the comparison of macadamia orchard edges. Species richness displayed in a), and two species diversity estimates with b) the exponential of Shannon's entropy index and c) the inverse of Simpson's concentration index, for the two edges (human-modified and natural) as well as the two defined seasons (high and low); the solid line shows the interpolated part whereas the dashed line shows the extrapolated part of the rarefaction curve; fainter colours show 95% confidence intervals of the curves.



**Fig. A.2.** Incidence based diversity estimates with respect to sample coverage (Hill numbers) for the comparison of the Nature Reserve with natural macadamia orchard edges. Species richness displayed in a), and two species diversity estimates with b) the exponential of Shannon's entropy index and c) the inverse of Simpson's concentration index, the solid line shows the interpolated part whereas the dashed line shows the extrapolated part of the rarefaction curve; fainter colours show 95% confidence intervals of the curves.

## References

- Ancillotto, L., Ariano, A., Nardone, V., Budinski, I., Rydell, J., Russo, D., 2017. Effects of free-ranging cattle and landscape complexity on bat foraging: implications for bat conservation and livestock management. *Agric. Ecosyst. Environ.* 241, 54–61.
- Ancillotto, L., Festa, F., De Benedetta, F., Cosentino, F., Pejic, B., Russo, D., 2021. Free-ranging livestock and a diverse landscape structure increase bat foraging in mountainous landscapes. *Agrofor. Syst.* 95 (2), 407–418.
- Barton, K., 2017. Multi-Model Inference. R package version 1.40.0. (<https://CRAN.R-project.org/package=MuMIn/>). (Accessed 14 March 2020).
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67 (1), 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Bontadina, F., Arlettaz, R., Fankhauser, T., Lutz, M., Mühlethaler, E., Theiler, A., Zingg, P., 2000. The lesser horseshoe bat *Rhinolophus hipposideros* in Switzerland: present status and research recommendations. *Le Rhinolophe* 14, 69–83.
- Cohen, Y., Bar-David, S., Nielsen, M., Bohmann, K., Korine, C., 2020. An appetite for pests: synanthropic insectivorous bats exploit cotton pest irruptions and consume various deleterious arthropods. *Mol. Ecol.* 29, 1185–1198. <https://doi.org/10.1111/mec.15393>.
- Colwell, R.K., 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. User's Guide and Application. (<http://purl.oclc.org/estimates>). (Accessed 3 February 2020).
- Cooper-Bohannon, R., 2016. Predicting bat distributions and diversity hotspots in southern Africa. *Hystrix Ital. J. Mamm.* <https://doi.org/10.4404/hystrix-27.1-11722>.
- Corben, C., 2006. AnalookW for bat call analysis using ZCA Titley Electronics, New South Wales, Australia. (<https://users.lmi.net/corben/>). (Accessed 3 December 2019).
- Costa, A., Silva, B., Jiménez-Navarro, G., Barreiro, S., Melguizo-Ruiz, N., Rodríguez-Pérez, J., Vasconcelos, S., Beja, P., Moreira, F., Herrera, J.M., 2019. Structural simplification compromises the potential of common insectivorous bats to provide biocontrol services against the major olive pest *Prays oleae*. *Agric. Ecosyst. Environ.* 287, 106708. <https://doi.org/10.1016/j.agee.2019.106708>.
- Denzinger, A., Schnitzler, H.U., 2013. Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. *Front. Physiol.* 4. <https://doi.org/10.3389/fphys.2013.00164>.
- Foord, S., Swanepoel, L., Evans, S., Schoeman, C., Schoeman, C., Keith, M., Erasmus, B., Smith, A., Mauda, E., Maree, N., Nembudani, L., Munyai, T., Taylor, P.J., 2018. Animal taxa contrast in their scale-dependent responses to land use change in rural Africa. *PLoS One* 13 (5), e0194336. <https://doi.org/10.1371/journal.pone.0194336>.
- Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global consequences of land use. *Science* 309 (5734), 570–574.
- Frey-Ehrenbold, A., Bontadina, F., Arlettaz, R., Obrist, M.K., 2013. Landscape connectivity, habitat structure and activity of bat guilds in farmland-dominated matrices. *J. Appl. Ecol.* 50, 252–261. <https://doi.org/10.1111/1365-2664.12034>.
- Frick, W.F., Puechmaile, S.J., Willis, C.K.R., 2016. White-nose syndrome in bats. In: Voigt, C.C., Kingston, T. (Eds.), *Bats in the Anthropocene: Conservation of Bats in a Changing World*. Springer International Publishing, Cham, pp. 245–262. [https://doi.org/10.1007/978-3-319-25220-9\\_9](https://doi.org/10.1007/978-3-319-25220-9_9).
- Ghanem, S.J., Voigt, C.C., 2012. Increasing Awareness of ecosystem services provided by bats. In: *Advances in the Study of Behavior*. Elsevier, pp. 279–302. <https://doi.org/10.1016/B978-0-12-394288-3.00007-1>.
- Hahn, N., 2017. An historic account of the extinct high rainfall grasslands of the Soutpansberg, South Africa. *Transactions of the Royal Society of South Africa.* (<https://doi.org/10.1080/0035919X.2017.1346528>).
- Heim, O., Treitler, J.T., Tschapka, M., Knörnschild, M., Jung, K., 2015. The importance of landscape elements for bat activity and species richness in agricultural areas. *PLoS One* 10 (7), e0134443.
- Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. *Biom. J.* 50 (3), 346–363.
- Hsieh, T.C., Ma, K.H., Chao, A., 2018. iNEXT: iNterpolation and EXTrapolation for species diversity. R package version 2.0.17. (<http://chao.stat.nthu.edu.tw/blog/software-download/>). (Accessed 2 December 2019).
- Jan, P.L., Zarzoso-Lacoste, D., Fourcy, D., Baudouin, A., Farcy, O., Boireau, J., Le Gouar, P., Puechmaile, S.J., Petit, E.J., 2020. Population-level sensitivity to landscape variables reflects individual-based habitat selection in a woodland bat species. *bioRxiv*. <https://doi.org/10.1101/752733>.
- Jones, K.E., Purvis, A., Gittleman, J.L., 2003. Biological correlates of extinction risk in bats. *Am. Nat.* 161, 601–614. <https://doi.org/10.1086/368289>.
- Jung, K., Threlfall, C.G., 2016. Urbanisation and its effects on bats—a global meta-analysis. In: Voigt, C.C., Kingston, T. (Eds.), *Bats in the Anthropocene: Conservation of Bats in a Changing World*. Springer International Publishing, Cham, pp. 13–33. [https://doi.org/10.1007/978-3-319-25220-9\\_2](https://doi.org/10.1007/978-3-319-25220-9_2).
- Kalda, O., Kalda, R., Liira, J., 2015. Multi-scale ecology of insectivorous bats in agricultural landscapes. *Agric. Ecosyst. Environ.* 199, 105–113. <https://doi.org/10.1016/j.agee.2014.08.028>.
- Karp, D.S., Daily, G.C., 2014. Cascading effects of insectivorous birds and bats in tropical coffee plantations. *Ecology* 95, 1065–1074. <https://doi.org/10.1890/13-1012.1>.
- Kelly, R.M., Kitzes, J., Wilson, H., Merenlender, A., 2016. Habitat diversity promotes bat activity in a vineyard landscape. *Agric. Ecosyst. Environ.* 223, 175–181. <https://doi.org/10.1016/j.agee.2016.03.010>.
- Kolkert, H.L., Smith, R., Rader, R., Reid, N., 2021. Prey removal in cotton crops next to woodland reveals periodic diurnal and nocturnal invertebrate predation gradients from the crop edge by birds and bats. *Sci. Rep.* 11, 5256. <https://doi.org/10.1038/s41598-021-84633-8>.
- Kunz, T.H., de Torre, Braun, Bauer, E., Lobova, D., Fleming, T.H., 2011. Ecosystem services provided by bats: ecosystem services provided by bats. *Ann. N. Y. Acad. Sci.* 1223, 1–38. <https://doi.org/10.1111/j.1749-6632.2011.06004.x>.
- Linden, V.M.G., Grass, I., Jobert, E., Tscharnke, T., Weier, S.M., Taylor, P.J., 2019. Ecosystem services and disservices by bats, birds and monkeys change with macadamia landscape composition. *J. Appl. Ecol.* 56 (8), 2069–2078. <https://doi.org/10.1111/1365-2664.13424>.
- Linden, V.M.G., Weier, S.M., Gaigher, I., Kuipers, H.J., Weterings, M.J.A., Taylor, P.J., 2014. Changes of bat activity, species richness, diversity and community composition over an altitudinal gradient in the Soutpansberg range, South Africa. *Acta Chiropt.* 16, 27–40. <https://doi.org/10.3161/150811014X683246>.
- López-Hoffman, L., Wiederholt, R., Sansone, C., Bagstad, K.J., Cryan, P., Diffendorfer, J. E., Goldstein, J., LaSharr, K., Loomis, J., McCracken, G., Medellín, R.A., Russell, A., Semmens, D., 2014. Market forces and technological substitutes cause fluctuations in

- the value of bat pest-control services for cotton. *PLoS One* 9, e87912. <https://doi.org/10.1371/journal.pone.0087912>.
- Lüdecke, D., Makowski, D., Waggoner, P., Patil I., 2020. Performance: assessment of regression models performance. R package version 0.4.6. (<https://CRAN.R-project.org/package=performance>). (Accessed 1 March 2020).
- Maas, B., Karp, D.S., Bumrungsri, S., Darras, K., Gonthier, D., Huang, J.C.-C., Lindell, C. A., Maine, J.J., Mestre, L., Michel, N.L., Morrison, E.B., Perfecto, I., Philpott, S.M., Şekercioğlu, Ç.H., Silva, R.M., Taylor, P.J., Tschamtkke, T., Van Bael, S.A., Whelan, C. J., Williams-Guillén, K., 2016. Bird and bat predation services in tropical forests and agroforestry landscapes: ecosystem services provided by tropical birds and bats. *Biol. Rev.* 91, 1081–1101. <https://doi.org/10.1111/brv.12211>.
- Miller, B.W., 2001. A method for determining relative activity of free flying bats using a new activity index for acoustic monitoring. *Acta Chiropt.* 3, 93–105.
- Monadjem, A., Taylor, P.J., Cotterill, F.P.D., (Woody), Schoeman, M.C., 2020. *Bats of Southern and Central Africa: a Biogeographic and Taxonomic Synthesis*, second ed. Wits University Press, Johannesburg.
- Mostert, T.H.C., Breidenkamp, G.J., Klopper, H.L., Verwey, C., Mostert, R.E., Hahn, N., 2008. Major vegetation types of the Soutpansberg Conservancy and the Blouberg Nature Reserve, South Africa. *Koedoe* 50, 32–48.
- Mtsetfwa, F., McCleery, R.A., Monadjem, A., 2018. Changes in bat community composition and activity patterns across a conservation-agriculture boundary. *Afr. Zool.* 53, 99–106. <https://doi.org/10.1080/15627020.2018.1531726>.
- Mucina, L., Rutherford, M.C., 2006. *The Vegetation of South Africa, Lesotho and Swaziland*. Strelitzia 19, South African National Biodiversity Institute, Pretoria, viii + 807.
- Parker, D.M., Bernard, R.T., 2018. The use of acoustic detectors for assessing bat species richness and functional activity in a South African National Park. *Mammalia* 83 (1), 53–63.
- Pinaud, D., Claireau, F., Leuchtman, M., Kerbirou, C., 2018. Modelling landscape connectivity for greater horseshoe bat using an empirical quantification of resistance. *J. Appl. Ecol.* 55, 2600–2611. <https://doi.org/10.1111/1365-2664.13228>.
- Puig-Montserrat, X., Mas, M., Flaquer, C., Tuneu-Corral, C., López-Baucells, A., 2021. Benefits of organic olive farming for the conservation of gleaning bats. *Agric. Ecosyst. Environ.* 313. <https://doi.org/10.1016/j.agee.2021.107361>.
- Rowse, E.G., Lewanzik, D., Stone, E.L., Harris, S., Jones, G., 2016. Dark matters: the effects of artificial lighting on bats. In: Voigt, C.C., Kingston, T. (Eds.), *Bats in the Anthropocene: Conservation of Bats in a Changing World*. Springer International Publishing, Cham, pp. 187–213. [https://doi.org/10.1007/978-3-319-25220-9\\_7](https://doi.org/10.1007/978-3-319-25220-9_7).
- Russo, D., Ancillotto, L., 2015. Sensitivity of bats to urbanization: a review. *Mamm. Biol.* 80, 205–212. <https://doi.org/10.1016/j.mambio.2014.10.003>.
- Russo, D., Bosso, L., Ancillotto, L., 2018. Novel perspectives on bat insectivory highlight the value of this ecosystem service in farmland: research frontiers and management implications. *Agric. Ecosyst. Environ.* 266, 31–38. <https://doi.org/10.1016/j.agee.2018.07.024>.
- Rydell, J., Nyman, S., Eklöf, J., Jones, G., Russo, D., 2017. Testing the performances of automated identification of bat echolocation call sequences: a request for prudence. *Ecol. Indic.* 78, 416–420.
- SAMAC, 2019. *Macadamia Industry* 2020. (<https://www.samac.org.za/industry-statistics/>). (Accessed 17 March 2021).
- Shapiro, J.T., Monadjem, A., Röder, T., McCleery, R.A., 2019. Response of bat activity to land cover and land use in savannas is scale-, season-, and guild-specific. *Biol. Conserv.* 241. <https://doi.org/10.1016/j.biocon.2019.108245>.
- Taylor, P.J., Monadjem, A., Nicolaas Steyn, J., 2013a. Seasonal patterns of habitat use by insectivorous bats in a subtropical African agro-ecosystem dominated by macadamia orchards. *Afr. J. Ecol.* 51, 552–561. <https://doi.org/10.1111/aje.12066>.
- Taylor, P.J., Sowler, S., Schoeman, M.C., Monadjem, A., 2013b. Diversity of bats in the Soutpansberg and Blouberg Mountains of northern South Africa: complementarity of acoustic and non-acoustic survey methods. *S. Afr. J. Wildl. Res.* 43, 12–26. <https://doi.org/10.3957/056.043.0117>.
- Toffoli, R., Rughetti, M., 2017. Bat activity in rice paddies: organic and conventional farms compared to unmanaged habitat. *Agric. Ecosyst. Environ.* 249, 123–129.
- Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D., Swackhamer, D., 2001. Forecasting agriculturally driven global environmental change. *Science* 292, 281–284.
- Tschamtkke, T., Clough, Y., Wanger, T.C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J., Whitbread, A., 2012. Global food security, biodiversity conservation and the future of agricultural intensification. *Biol. Conserv.* 151 (1), 53–59.
- UNESCO, 2010. *MAB Biosphere Reserves Directory*, Biosphere Reserve Information, South Africa, Vhembe. (<http://www.unesco.org>). (Accessed 3 February 2020).
- Van Wyk, A.E., Smith, G.F., 2001. *Regions of floristic endemism in southern Africa: a review with emphasis on succulents*. Umdaus Press, South Africa.
- Wanger, T.C., Darras, K., Bumrungsri, S., Tschamtkke, T., Klein, A.M., 2014. Bat pest control contributes to food security in Thailand. *Biol. Conserv.* 171, 220–223.
- Weier, S.M., Grass, I., Linden, V.M.G., Tschamtkke, T., Taylor, P.J., 2018. Natural vegetation and bug abundance promote insectivorous bat activity in macadamia orchards, South Africa. *Biol. Conserv.* 226, 16–23. <https://doi.org/10.1016/j.biocon.2018.07.017>.
- Weier, S.M., Linden, V.M.G., Gaigher, I., White, P.J.C., Taylor, P.J., 2016. Changes of bat species composition over altitudinal gradients on northern and southern aspects of the Soutpansberg mountain range, South Africa. *Mammalia* 81. <https://doi.org/10.1515/mammalia-2015-0055>.
- Wickham, H., 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York.
- Wickramasinghe, L.P., Harris, S., Jones, G., Vaughan, N., 2003. Bat activity and species richness on organic and conventional farms: impact of agricultural intensification. *J. Appl. Ecol.* 40, 984–993. <https://doi.org/10.1111/j.1365-2664.2003.00856.x>.
- Wordley, C.F.R., Sankaran, M., Mudappa, D., Altringham, J.D., 2017. Bats in the Ghats: Agricultural intensification reduces functional diversity and increases trait filtering in a biodiversity hotspot in India. *Biol. Conserv.* 210, 48–55. <https://doi.org/10.1016/j.biocon.2017.03.026>.