



Using species distribution models to gauge the completeness of the bat checklist of Eswatini

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Abstract

National species checklists are important for a variety of reasons, including biodiversity conservation. However, these national checklists are rarely complete, and it is not easy to gauge how many species have been overlooked or what the taxonomic identities of overlooked species would be. This is particularly the case for small, elusive, or nocturnal species such as bats. Despite their diversity and importance as ecosystem service providers, bat distributions are poorly known throughout much of Africa. We present a national checklist of bats for a small African country, Eswatini, by compiling species from museum specimens and literature records. A total of 32 species of bats have been recorded from the country. Since 1995, new species have continued to be recorded in Eswatini, with five additional species added since the last published checklist in 2016, suggesting that some species may still be overlooked. In order to determine what species these may be, we used species distribution models based on the occurrence records of bats from southern Africa to predict what species would occur in Eswatini, which was then compared with what has been collected and deposited in museums. Our models predicted that a total of 47 species are likely to occur in Eswatini compared with 32 species collected to date. Our data suggest that the national checklist of bats of Eswatini is not yet complete and that further species are expected to be recorded for the country. We suggest that species distribution models can be useful for gauging the completeness of national checklists and predicting which species may have been overlooked.

Keywords Chiroptera · Maxent · Species area curve · Species richness

Introduction

Country checklists of species may serve several important functions, one of which is to inform conservation decisions.

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However, checklists are rarely complete as new species are discovered or described within the boundaries of even the most well-surveyed countries. While African countries support a high known diversity of mammal species (Kingdon et al. 2013), this is also the continent predicted to have the greatest number of undescribed mammal taxa in the world (Fisher et al. 2018), and vast regions of the continent have not been surveyed at all for small mammals (Monadjem et al. 2010a, 2015). Even in well-surveyed parts of the continent, such as South Africa, making sense of species distributions is often difficult because of sampling bias, with accessibility being a critical factor in where past surveys have been conducted (Reddy and Davalos 2003). In other words, remote or inaccessible areas are typically under-represented in surveys.

Bats (order Chiroptera) are the second most diverse order of mammals after rodents (Simmons 2005), with over 1400 species currently reported (Burgin et al. 2018; Simmons and Cirranello 2018) of which around 314 species (22% of the global total) occur in Africa (ACR 2019). Bats are

frequently used in conservation planning exercises and are specifically targeted in many biodiversity surveys (Decher et al. 2001; Fahr and Ebigo 2003; Monadjem and Fahr 2007; Monadjem et al. 2016). Their importance for providing ecosystem services is also now well documented (Boyles et al. 2011; Kunz et al. 2011; Taylor et al. 2018a). Yet knowledge of bat distributions remains relatively poor compared with many other mammalian groups (Herkt et al. 2016), even in well-surveyed regions. For example, *Myotis alcaethoe* was added to the UK's national checklist only in 2010 (Jan et al. 2010) increasing the total number of resident species to 17 (Dietz and von Helversen 2004), and *Pipistrellus pygmaeus* was added in the decade before that (Barratt et al. 1997; Mayer and von Helversen 2001). This illustrates that even in a country like the UK with dozens of bat biologists and thousands of dedicated volunteers undertaking annual bat surveys (Mitchell-Jones et al. 1993) (also see <https://www.bats.org.uk/our-work/national-bat-monitoring-programme/reports/nbmp-annual-report>), new country records can still be made. In contrast, many tropical countries have a severe shortage of bat biologists or bat volunteers (Taylor 1999), with many African countries having no more than one or two dedicated professional bat biologists (A. Monadjem, personal observation).

In Africa, only a few countries have recent national checklists (Monadjem and Fahr 2007; Monadjem et al. 2010b; Bates et al. 2013; Amori et al. 2016; Child et al. 2016; Musila et al. 2019). For many countries, national checklists are not available, fragmentary in nature (having been published in numerous unrelated papers) or decades old (Kock 1969; Ansell 1978; Schlitter et al. 1982; Happold et al. 1987; Crawford-Cabral 1989; Yalden et al. 1996). While tools like distribution maps from the IUCN Red List (<https://www.iucnredlist.org/>) are available for Africa and used for ecological studies, they tend to underestimate species' ranges and the biodiversity of any given geographical area (Herkt et al. 2017).

In Eswatini (formerly Swaziland), bat surveys can be categorized as "historical" (pre-1995) or recent (since 1995) (see Methods). Prior to 1995, 12 species had been collected from the country and deposited in museums in South Africa and the UK (Monadjem 1998). However, the first checklist of bats in Eswatini was only published in 1997, and mostly based on surveys conducted from 1995 onward, it listed 16 species (Monadjem 1997)(Table 1). A year later, the total number of species recorded in Eswatini increased to 19 (Monadjem 1998). By 2005, one additional species had been added to the national list (Monadjem 2005), and by this date, all the species collected prior to 1995 had been captured in recent surveys (Monadjem et al. 2005). The next published update affecting the bat checklist of the country was in 2008, when five new species were added (Monadjem and Reside 2008), raising the national total to 25 species. The last published

Table 1 Bioclimatic and other environmental variables with variance inflation factor (VIF) < 10, which were used in the Maxent models for bat distributions in this study

Variable	Description	VIF
Alt	Altitude	5.10
Alt_rough	Altitudinal roughness	1.40
Ecoregions	Ecoregions	1.53
Bio_2	Mean diurnal range	2.39
Bio_3	Isothermality	2.95
Bio_8	Mean temperature of wettest quarter	2.26
Bio_9	Mean temperature of driest quarter	7.72
Bio_13	Precipitation of wettest month	5.09
Bio_14	Precipitation of driest month	3.32
Bio_15	Precipitation seasonality	2.99
Bio_18	Precipitation of warmest quarter	2.89
Bio_19	Precipitation of coldest quarter	1.90

checklist of Eswatini was in 2016 and listed 26 species (Shapiro and Monadjem 2016), but this paper erroneously omitted *Tadarida aegyptiaca*, which had been recorded previously (Monadjem 1998), and hence should have listed 27 species.

Clearly, the number of bat species recorded in Eswatini has risen significantly through time, raising doubts as to the completeness of this national checklist. This paper aims to assess how complete the current checklist is and to predict which species may have been overlooked. This is achieved by comparing the actual number of species recorded in the country with species predicted based on species distribution models.

Materials and methods

Study area

Eswatini is a small country situated in southern Africa covering an area of 17,360 km². The country is topographically varied, with the Drakensberg mountain range in the west and the Lubombo mountain range on the eastern border with Mozambique. In between these two mountain ranges is a lowland region (Fig. 1). The western highlands comprise montane grassland with patches of forest, whereas the rest of the country is mostly covered in savanna (Monadjem et al. 2003).

Species data

We compiled a dataset of all the bats collected in Eswatini based on historical pre-1995 collections and recent post-1995 records. All records were collected by A. Monadjem and various colleagues and students (for references to the

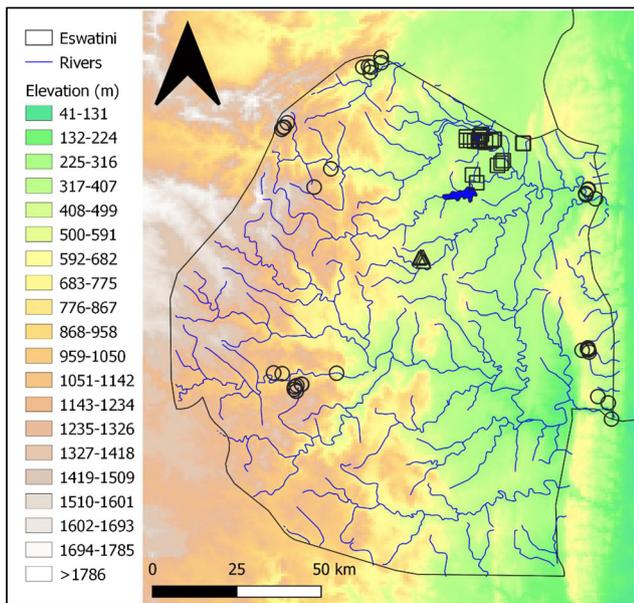


Fig. 1 A digital elevation map of Eswatini showing the relief of the country including the major rivers flowing through. Also shown are the study sites in Eswatini at which new bat species not mentioned in Shapiro and Monadjem et al. (2016) have been recorded. Squares, Inyoni Yami Swaziland Irrigation Scheme (IYSIS) survey; circles, Strengthening the National Protected Areas System of Swaziland (SNAP) survey; triangles, Dombeya Game Reserve survey (see Methods for further details)

various publications see the Introduction). For the post-1995 dataset, we compiled the year in which each species was first recorded in the country and a cumulative total number of species for the period 1995–2018.

New bats recorded in Eswatini since 2015 have not yet been published and are presented here based on extensive trapping surveys conducted at (1) Inyoni Yami Swaziland Irrigation Scheme cattle ranch (IYSIS, September 2015 to April 2016) near Tshaneni in northern Eswatini; (2) nine sites across the central and northern parts of the country under the Strengthening National Protected Areas project (SNPAS, December 2016 to February 2017); and (3) Dombeya Game Reserve (January 2018) (Fig. 1). Bats were captured using standard methods including setting up of mist nets and harp traps as described in Monadjem and Reside (2008). Voucher specimens of each species were collected and deposited in the Eswatini National Museum of Natural History, which were subsequently identified based on Monadjem et al. (2020a). Taxonomy follows Monadjem et al. (2020a) except for recent changes to the pipistrelle-like bat species (Monadjem et al. 2020b).

Beyond Eswatini, bat specimen records were obtained from Monadjem et al. (2020a) which included 125 species and 6344 unique locality records from southern Africa (Fig. 2). We reduced this database in size by removing all species with less than six unique locality records in the region ($n = 32$ species). We further reduced the dataset by removing duplicate occurrence records for the same species within a pixel

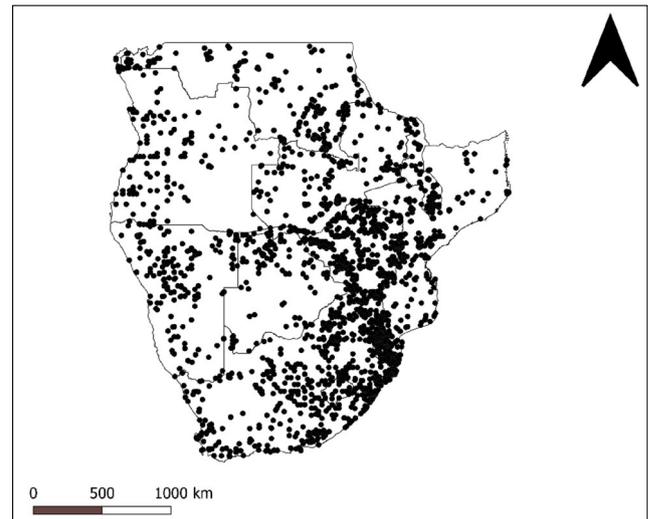


Fig. 2 Map of the southern African region showing all the bat specimens with georeferenced localities used in this study

(2.5 arc min, see below) (see Table S1 for the number of occurrence points per species used in this study). This dataset was then used to model distributions of bat species occurring in the region. Our choice of this region was based on three considerations: (1) this is a vast region comprising diverse landscapes to the south of the main rainforest bloc of the Congo basin where the taxonomy of bats is relatively well known and stable; (2) many of the bats occurring in southern Africa are endemic or near-endemic to this region, and hence the entire distribution of nearly all bat species that occur in Eswatini is encompassed by this region; and (3) this region is relatively well surveyed compared with other parts of Africa, and distributional records have been published (Monadjem et al. 2020a).

Species distribution modeling and statistical analysis

We modeled the predicted suitable environmental space of species using Maxent version 4.1.1 (Phillips et al. 2006; Phillips et al. 2020). Models were run at a resolution of approximately 5 km (2.5 arc min) using BIOCLIM variables from the WorldClim database (Hijmans et al. 2005), as well as altitude (Hijmans et al. 2005), altitudinal roughness extracted from altitude using the program DIVA-GIS (available at www.divagis.org), and ecoregions as classified by Olson et al. (2001). Since BIOCLIM variables are frequently strongly correlated, we assessed the correlation between these variables in the R package “usdm” (Naimi et al. 2014). We did this in two ways: (1) excluding one variable in every pair of variables with $r \geq 0.8$ by removing the one with the higher variance inflation factor (VIF) using the function “vifcor” and (2) removing variables with VIF >10 using the function “vifstep” (Soulтан et al. 2019). Both methods resulted in the inclusion of the same 12 variables, which are presented in Table 1.

We ran Maxent models in R version 3.6.2 (R Core Team 2019) using the package “dismo” (Hijmans et al. 2013). We used hinged and categorical variables that smooth variable responses and generally improve model performance (Phillips and Dudík 2008; Merow et al. 2013). We divided bat species occurrence records from southern Africa into training (75%) and test (25%) datasets. The selection of the geographical background has important implications for the results of species distribution models (Acevedo et al. 2012; Phillips et al. 2009); a suitable background reflects the geographical space available to the species by dispersal (Zhu et al. 2014). Therefore, for each species, we randomly sampled 10,000 background points from 100 km circular buffers around all occurrence points for that species. We used the value of 100 km because this is the distance that *Nycteris thebaica* (a particularly sedentary, clutter-foraging bat species) is able to cover during dispersal (Monadjem 2006), and therefore, this buffered range would represent the minimum area available to any of the bat species we included in our analyses (Merow et al. 2013). We tested each model with the area under the receiver operating characteristic curve (AUC) statistic, which ranges from 0 to 1 with higher values signifying a better fit (Merow et al. 2013); values equal to or less than 0.5 indicate models no better than random, while values greater than 0.75 represent good model fit (Elith et al. 2006). We used the same 12 environmental variables (Table 1) and Maxent parameters for all species (Cooper-Bohannon et al. 2016). We converted the predicted model outputs from Maxent (probabilities of suitability) into “presence-absence” maps using species-specific thresholds that maximized the sum of sensitivity and specificity, which is appropriate for presence-only data (Liu et al. 2013). We summed the modeled distributions of all the bats to quantify species richness using the “Raster Calculator” in QGIS (QGIS Development Team 2020).

We extracted all unique locality records for bats in Eswatini ($n = 231$ locality records) and prepared a species richness map for the country using the “Point to Grid” tool in DIVA-GIS based on a “quarter-degree” grid size that is $0.25^\circ \times 0.25^\circ$ in extent (approximately 24 km in length) (Hijmans et al. 2012). To test for a relationship between sampling effort (number of specimens captured) and species richness, we ran a linear regression using the “Analysis” function in DIVA-GIS.

A regression of the bat species richness against area of southern African countries (south of the Zambezi-Kunene Rivers) was conducted in the program R version 3.6.2 (R Core Development Team 2019).

Results

The checklist of bat species in Eswatini has risen steadily over time from 12 species pre-1995 to 32 species at present (Table 2)(Fig. 3). This increase, however, has not been at a constant pace, with two short periods of stasis in the late 1990s and

early 2000s and one longer period of stasis from 2007 to 2013 (Fig. 3).

Although bats have been surveyed relatively widely in Eswatini, collecting effort has been skewed to just a few areas, particularly the northeast and northwest regions, while surveys have been more limited in the southern half of the country (Fig. 4). At a quarter-degree scale, only one complete grid had not been surveyed by 2018 (located in the center of the country), as well as four partial grids on the borders of South Africa and Mozambique (two of which fall mostly outside of Eswatini) (Fig. 4). Based on this species richness map (Fig. 4), richness seems to vary considerably from grid to grid but is much lower in the southern half of the country compared to the north. The number of species per grid is also low, ranging from 1–3 species in much of the south to a maximum of 20 species in the northeast (Fig. 4). There was a strong correlation between species richness and sampling effort ($F = 17900$, $DF = 1022$, $R^2 = 0.946$).

However, the modeled species richness presents a different pattern (Fig. 5); the performance of each species model is presented in Table S1. On a regional scale, species richness is highest in the southern seaboard of South Africa, north through Eswatini into Zimbabwe, central Mozambique, and southern Malawi (Fig. 5a). Across the southern African region, species richness ranged from 1 to 43 species per pixel. When focusing on Eswatini, it is apparent that species richness is not uniformly high across the country (Fig. 5b). Modeled species richness was highest in the north-central parts of the country (reaching a maximum of 41 species per pixel), with a spur of high richness extending south along the boundary zone between high and low-lying regions of the country (see Fig. 1 for a digital elevation map of the country). Compared with the northern half of the country, species richness was generally lower in southern Eswatini (maximum of 35 species per pixel), especially in the southwest where richness was mostly between 11 and 15 species per pixel; the extreme west of the country also had low species richness (Fig. 5b). The median number of species per pixel in Eswatini was 21, and just 17 pixels supported less than 15 species of bats, while 29 pixels support more than 35 species (Fig. S1). The total number of bat species estimated to occur in Eswatini based on species distribution models was 47 species, compared with the 32 species that have been recorded to date (Table S2).

There was a positive relationship between the area of southern African countries and the number of bats species recorded within them (Fig. S2). Based on this regression, the number of species predicted to occur in Eswatini is 34–35 species, which is 2–3 species more than currently recorded, and about 10 species less than that predicted from modeling distributions (Table S2).

A total of five species are reported for the first time in Eswatini since the last published national checklist of bats (Shapiro and Monadjem 2016). Additional details of the

Table 2 The national checklist of bats of Eswatini listing all 32 species that have been collected in the country with confirmed identifications, including their global conservation status (IUCN 2019)

Family	Genus	Species	IUCN status	Pre-1995	1997	1998	2005a	2005b	2008	2016	2020
Pteropodidae	<i>Epomophorus</i>	<i>crypturus</i>	LC		1						
Pteropodidae	<i>Epomophorus</i>	<i>wahlbergi</i>	LC	1	1						
Hipposideridae	<i>Hipposideros</i>	<i>caffer</i>	LC	1	1						
Rhinonycteridae	<i>Cloeotis</i>	<i>percivali</i>	LC	1			1				
Rhinolophidae	<i>Rhinolophus</i>	<i>blasii</i>	LC					1			
Rhinolophidae	<i>Rhinolophus</i>	<i>clivosus</i>	LC	1	1						
Rhinolophidae	<i>Rhinolophus</i>	<i>darlingi</i>	LC		1						
Rhinolophidae	<i>Rhinolophus</i>	<i>rhodesiae</i>	NE								1
Rhinolophidae	<i>Rhinolophus</i>	<i>simulator</i>	LC	1		1					
Emballonuridae	<i>Taphozous</i>	<i>mauritanus</i>	LC			1					
Nycteridae	<i>Nycteris</i>	<i>thebaica</i>	LC	1	1						
Molossidae	<i>Chaerephon</i>	<i>pumilus</i>	LC	1	1						
Molossidae	<i>Mops</i>	<i>condylurus</i>	LC	1	1						
Molossidae	<i>Mops</i>	<i>midas</i>	LC							1	
Molossidae	<i>Tadarida</i>	<i>aegyptiaca</i>	LC	1		1					
Miniopteridae	<i>Miniopterus</i>	<i>fraterculus</i>	LC			1					
Miniopteridae	<i>Miniopterus</i>	<i>natalensis</i>	LC		1						
Vespertilionidae	<i>Afronycteris</i>	<i>nana</i>	LC	1	1						
Vespertilionidae	<i>Eptesicus</i>	<i>hottentotus</i>	LC								1
Vespertilionidae	<i>Kerivoula</i>	<i>argentata</i>	LC								1
Vespertilionidae	<i>Kerivoula</i>	<i>lanosa</i>	LC						1		
Vespertilionidae	<i>Laephotis</i>	<i>capensis</i>	LC	1	1						
Vespertilionidae	<i>Myotis</i>	<i>bocagii</i>	LC							1	
Vespertilionidae	<i>Myotis</i>	<i>tricolor</i>	LC						1		
Vespertilionidae	<i>Myotis</i>	<i>welwitschii</i>	LC								1
Vespertilionidae	<i>Neoromicia</i>	<i>anchietae</i>	LC						1		
Vespertilionidae	<i>Neoromicia</i>	<i>zuluensis</i>	LC						1		
Vespertilionidae	<i>Nycticeinops</i>	<i>schlieffeni</i>	LC		1						
Vespertilionidae	<i>Pipistrellus</i>	<i>hesperidus</i>	LC			1					
Vespertilionidae	<i>Pipistrellus</i>	<i>rusticus</i>	LC								1
Vespertilionidae	<i>Scotophilus</i>	<i>dinganii</i>	LC	1	1						
Vespertilionidae	<i>Scotophilus</i>	<i>viridis</i>	LC						1		

LC least concern, NE not evaluated. Also shown are the dates of first mention of each species in the literature: “1997,” Monadjem (1997); “1998,” Monadjem (1998); “2005a,” Monadjem et al. (2005); “2005b,” (Monadjem 2005); “2008,” Monadjem and Reside (2008); “2016,” Shapiro and Monadjem (2016); “2020,” this study

collecting localities and number of individuals captured for each of these species are provided in Table S3.

Discussion

In this paper, we present an updated checklist of the bats of Eswatini, which includes 32 species, an increase of five species from the most recent checklist (Shapiro and Monadjem 2016). This is lower than the species richness of many of the countries in the region. For example, Angola has 73 species (Taylor et al.

2018b), Mozambique 67 species (Monadjem et al. 2010b; Neves et al. 2018), Zambia 65 species, South Africa 63 species (Child et al. 2016), and Zimbabwe and Malawi both 62 species (Monadjem et al. 2020a). However, these countries are far larger than Eswatini, and this difference accounts for most of the disparity. Correcting for surface area, the number of species recorded from Eswatini to date is 2–3 species less than what is predicted from its area alone (Fig. S2).

The relatively rapid addition of new bat species to the Eswatini checklist, including the five species added since 2016 (Table 1, S3), suggests that this latest checklist (of 32

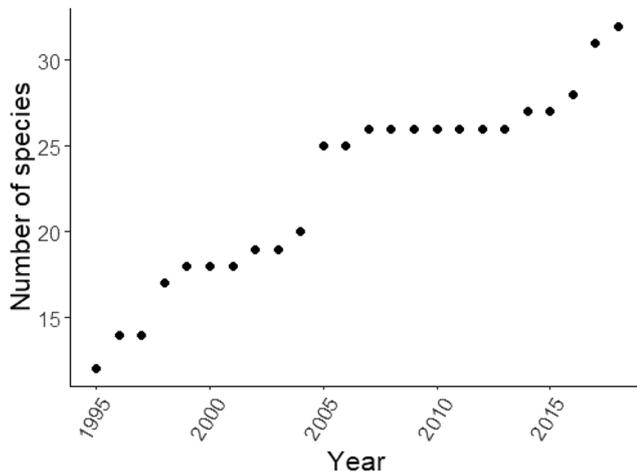


Fig. 3 Species accumulation curve showing the increase in species richness over time from 1995 to 2018 in Eswatini

species) is also incomplete. It is important to note that none of the additional species added to the checklist since 1995 are due to taxonomic rearrangements or recent splitting of species complexes. In every case, the additions were due to the discovery of a previously unrecorded species for the country, demonstrating the importance of field surveys. Taxonomic instability is unlikely to affect the bat fauna of a country as small as Eswatini since most African bat species complexes constitute two or more populations of non-overlapping taxa (Taylor et al. 2012; Monadjem et al. 2013, 2019). Hence,

based on the continuous accumulation of new species, we expect the country total to continue to rise as further field surveys are conducted.

Our species distribution models also point to likely overlooked bat species in Eswatini. Based on our Maxent models, some additional 15 species could perhaps occur in Eswatini since there seems to be suitable environmental conditions for them in the country. It is important to note that our predicted species richness map for southern Africa is very similar to those previously published for the region (Schoeman et al. 2013; Cooper-Bohannon et al. 2016; Herkt et al. 2016), giving us confidence in our species distribution models. The 15 yet-unrecorded bat species that our models predict to occur in Eswatini have been recorded at distances ranging from 1 to 800 km (Table 3) from the Eswatini border. This suggests that their occurrences in the country are not equally probable; those species occurring closer to the border are more likely to occur than those that are only known to occur much farther away. Furthermore, taking into consideration the ecology of each species can help determine the likelihood that it occurs in Eswatini. For example, in addition to suitable climate and elevation, the availability of habitat and roosts would also affect a species' probability of occurrence in the country. Migration is another useful factor to consider since migratory species are more likely to turn up at distant localities. Finally, taxonomic uncertainties may affect distribution models because the occurrence points used in making

Fig. 4 The distribution of all bat specimens collected in Eswatini (dots) laid over a “quarter-degree” grid ($0.25^\circ \times 0.25^\circ$) showing the number of bat species recorded within each grid

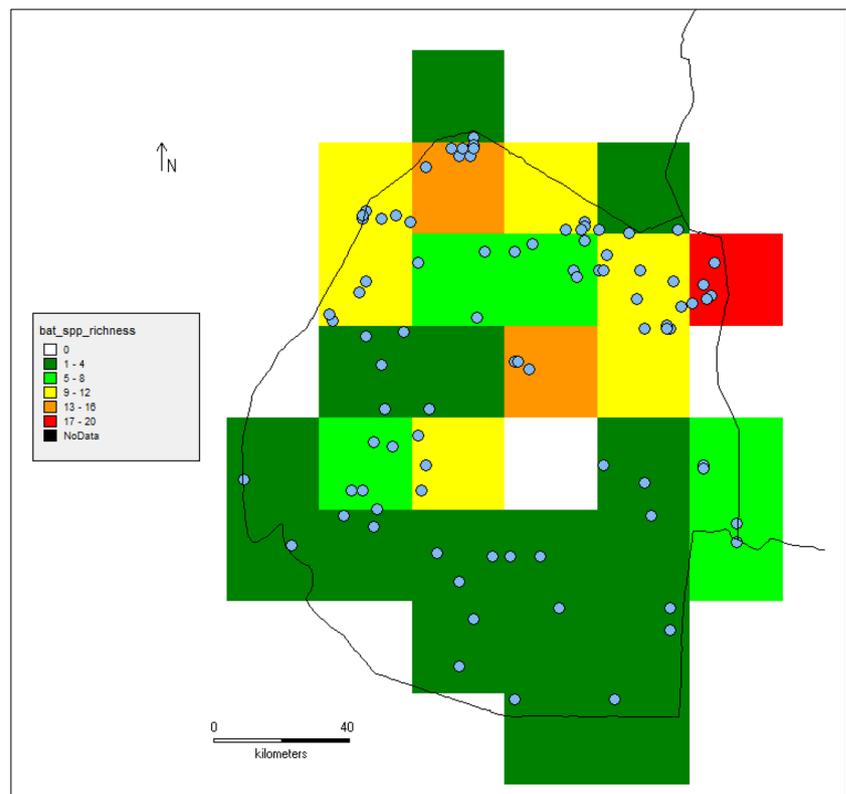
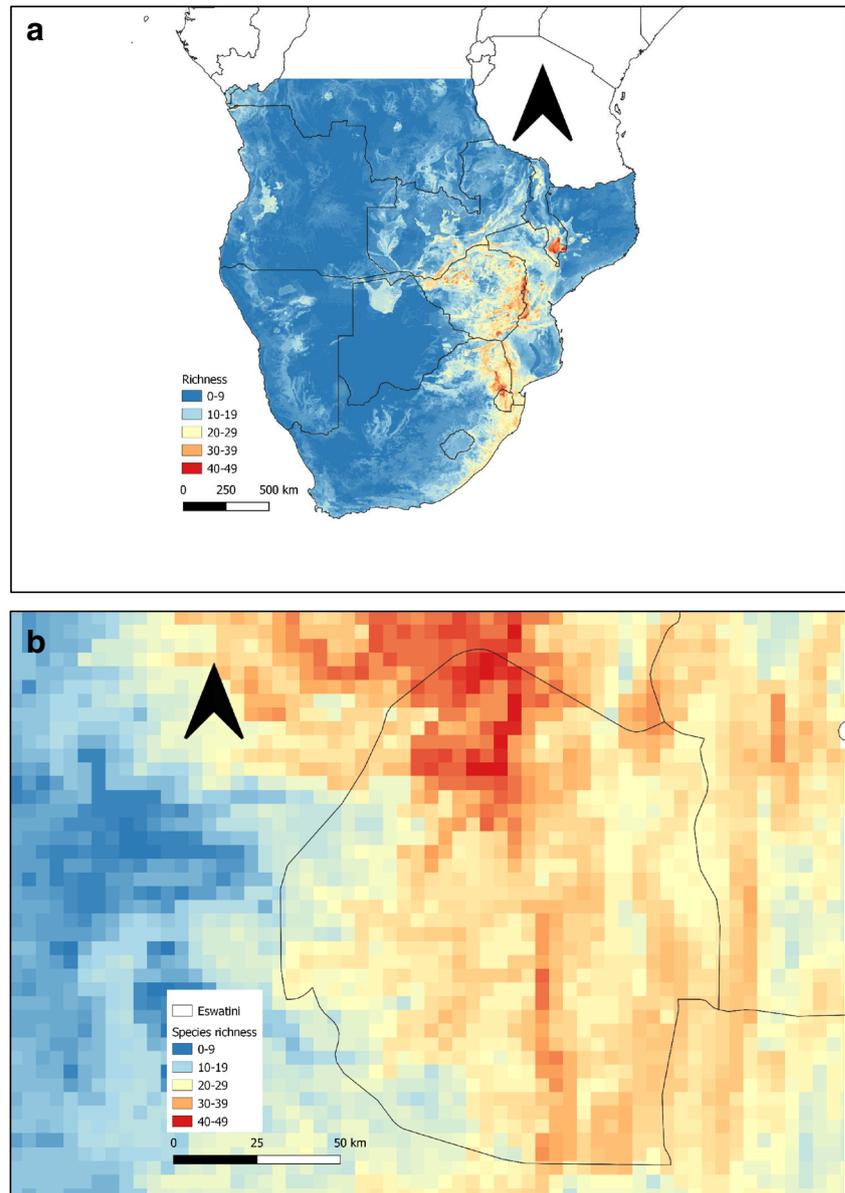


Fig. 5 Maps showing predicted species richness of bats based on Maxent models: **(a)** for southern Africa as defined in this study (following Monadjem et al. 2020a) and **(b)** for Eswatini. Note that the map presented in **(b)** is simply a zoomed in section of **(a)**



the predictions may in fact refer to more than one species, affecting the resulting predicted distributions.

Based on these factors (see Table 3), we predict that three of the 15 species (*Taphozous perforatus*, *Chaerephon ansorgei*, and *Eidolon helvum*) have a high chance of occurring in Eswatini because the nearest records are < 65 km from the border, and suitable habitat and roosts are available in the country. Another five species (*Otomops martiensseni*, *Rousettus aegyptiacus*, *Rhinolophus cohenae*, *Laephotis botswanae*, and *Pseudoromicia rendalli*) have a medium likelihood of occurrence based on closest records either being > 100 km away or <100 km but lacking suitable roosting sites in Eswatini. For example, Eswatini does not have the geology for the creation of large caves (Monadjem et al. 2003), and thus cave-roosting species, such as *Rousettus*

aegyptiacus or *Rhinolophus cohenae*, are unlikely to occur. The remaining seven species have not been recorded within close distance of Eswatini, and/or suitable habitat does not appear to be present in the country, and we therefore suggest that the probability of finding these species in Eswatini is rather low.

It is interesting to note that four of the five newly added species to the Eswatini bat checklist belong to the diverse family Vespertilionidae and the fifth belongs to the Rhinolophidae (Table S3). Two of the five species, *Rhinolophus rhodesiae* and *Kerivoula argentata*, were recorded within 2 km of the national border and without any further data may be assumed to have distributions marginal within the country. However, the remaining three species (*Eptesicus hottentotus*, *Myotis welwitschii*, and *Pipistrellus rusticus*)

Table 3 The 15 species of bats predicted to occur in Eswatini but not yet recorded by vouchered museum specimens

Family	Species	Closest record (km)	Habitat available	Status	Roost type	Taxonomic uncertainty	Chance of occurrence
Emballonuridae	<i>Taphozous perforatus</i>	1	Yes	Resident	Crevice	No	High
Molossidae	<i>Chaerephon ansorgei</i>	40	Yes	Resident	Crevice	No	High
Pteropodidae	<i>Eidolon helvum</i>	64	Yes	Migratory	Tree	No	High
Molossidae	<i>Otomops martiensseni</i>	250	Yes	Resident	Crevice	No	Medium
Pteropodidae	<i>Rousettus aegyptiacus</i>	55	Yes	Migratory	Cave	No	Medium
Rhinolophidae	<i>Rhinolophus cohenae</i>	35	Yes	Resident	Cave	No	Medium
Vespertilionidae	<i>Laephotis botswanae</i>	280	Yes	Resident	Tree	No	Medium
Vespertilionidae	<i>Pseudoromicia rendalli</i>	110	?	Resident	Tree	No	Medium
Miniopteridae	<i>Miniopterus mossambicus</i>	680	?	Resident	Cave	No	Low
Nycteridae	<i>Nycteris macrotis</i>	275	Yes	Resident	Cave	No	Low
Rhinolophidae	<i>Rhinolophus smithersi</i>	350	?	Resident	Cave	No	Low
Vespertilionidae	<i>Nycticeinops grandidieri</i>	800	No	Resident	Tree	Yes	Low
Vespertilionidae	<i>Scotoecus albofiscus</i>	70	No	Resident	Tree	No	Low
Vespertilionidae	<i>Scotoecus hindei</i>	130	?	Resident	Tree	Yes	Low
Miniopteridae	<i>Miniopterus inflatus</i>	30	?	Resident	Cave	Yes	Low

Included are other details that may have an impact on whether they will occur in the country. Closest record, distance from the record to the border of Eswatini (from Monadjem et al. 2020a); habitat available, whether suitable habitat is available in Eswatini; status, migratory or resident; roost, tree, cave, or crevice roosting; taxonomic uncertainty, yes indicates that the species or species group requires revision that may affect the naming of species in the region; chance of occurrence, scored as low, medium, or high based on this information

were captured well away from any border, suggesting that they may occur more widely in the country.

In conclusion, our study presents a bat checklist that includes 32 species in Eswatini, with up to 15 additional species that may still be recorded in the country. We suggest that species distribution models are a useful tool in gauging how complete national checklists are and identifying specific taxa that may have been overlooked, providing important baseline information to guide future conservation, management, and research strategies at both the national and regional level (Bungartz et al. 2011, Amori et al. 2012).

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Declarations

Conflict of interest The authors declare no competing interests. **Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10344-021-01463-9>.

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