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 the country, with five additional species added since the last published checklist in 2016, suggesting that some species may have still been 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 in gauging the completeness of national checklists and in 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. 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 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 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 Ebigbo 2003, Monadjem and Fahr 2007, Monadjem et al. 2016). Their importance for providing ecosystem services are 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 alcathoe* was added to the United Kingdom'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 United Kingdom 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 United Kingdom (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 species (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 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.

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

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 km^2. 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).

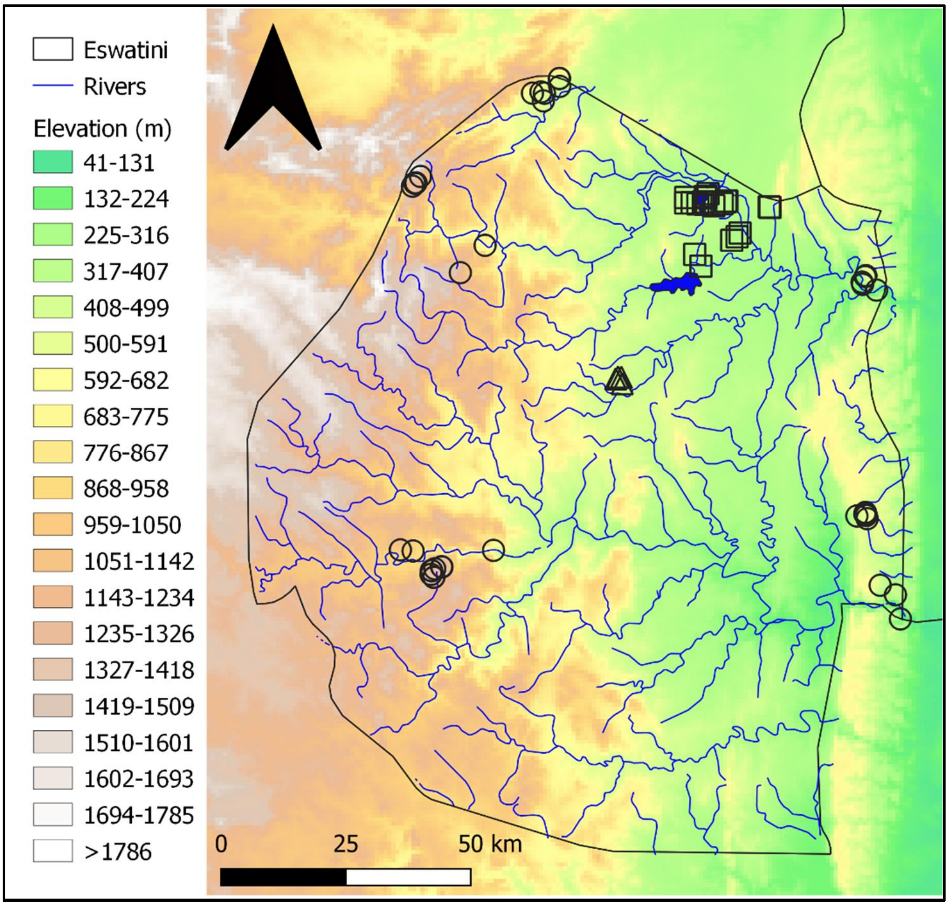

Fig. 1 – A digital elevation map of Eswatini showing the relief of the country including the major rivers flowing through. Also shown are the study sites in Eswatini at which new bat species not mentioned in Shapiro and Monadjem (2016) have been recorded. Squares = Inyoni Yami Swaziland Irrigation Scheme (IYSIS) survey;

circles = Strengthening the National Protected Areas System of Swaziland (SNAP) survey; triangles = Dombeya Game Reserve survey (see Methods for further details)

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 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 6,344 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 (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).

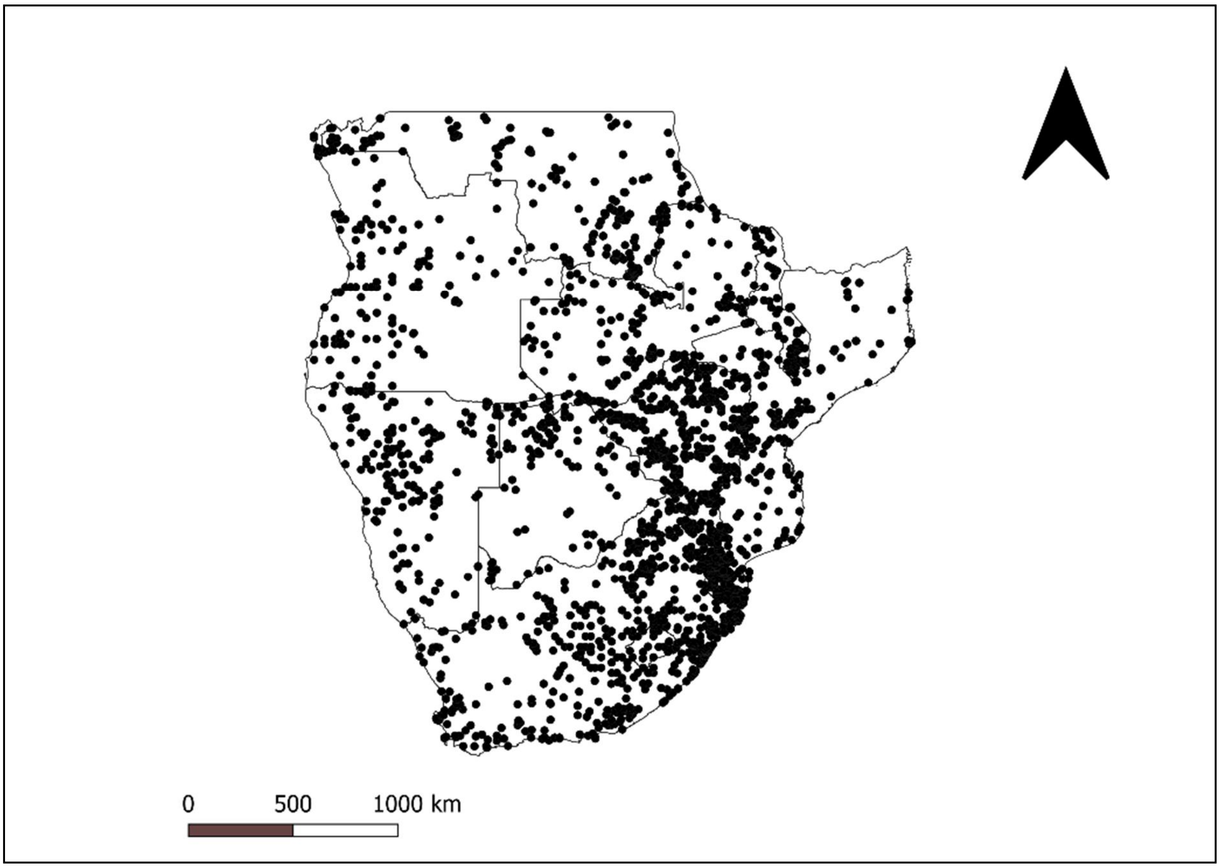

Fig. 2 – Map of the southern African region showing all the bat specimens with georeferenced localities used in this study

Species distribution modeling and statistical analysis

We modelled 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' (Soultan 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 Dudik 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 modelled 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 an actual species richness map for the country using the ‘Point to Grid’ tool in DIVA-GIS based on a “quarter-degree” grid size that is actually 0.25° × 0.25° 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).

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): 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

Family	Genus	Species	IUCN status	Pre-1995	1997	1998	2005a	2005b	2008	2016	2020
Pteropodidae	*Epomophorus*	*crypturus*	LC		1						
Pteropodidae	*Epomophorus*	*wahlbergi*	LC	1	1						
Hipposideridae	*Hipposideros*	*caffer*	LC	1	1						
Rhinonycteridae	*Cloeotis*	*percivali*	LC	1			1				
Rhinolophidae	*Rhinolophus*	*blasii*	LC					1			
Rhinolophidae	*Rhinolophus*	*clivosus*	LC	1	1						
Rhinolophidae	*Rhinolophus*	*darlingi*	LC		1						
Rhinolophidae	*Rhinolophus*	*rhodesiae*	NE								1
Rhinolophidae	*Rhinolophus*	*simulator*	LC	1		1					
Emballonuridae	*Taphozous*	*mauritianus*	LC			1					
Nycteridae	*Nycteris*	*thebaica*	LC	1	1						
Molossidae	*Chaerephon*	*pumilus*	LC	1	1						
Molossidae	*Mops*	*condylurus*	LC	1	1						
Molossidae	*Mops*	*midas*	LC							1	
Molossidae	*Tadarida*	*aegyptiaca*	LC	1		1					
Miniopteridae	*Miniopterus*	*fraterculus*	LC			1					
Miniopteridae	*Miniopterus*	*natalensis*	LC		1						
Vespertilionidae	*Afronycteris*	*nana*	LC	1	1						
Vespertilionidae	*Eptesicus*	*hottentotus*	LC								1
Vespertilionidae	*Kerivoula*	*argentata*	LC								1
Vespertilionidae	*Kerivoula*	*lanosa*	LC						1		
Vespertilionidae	*Laephotis*	*capensis*	LC	1	1						

Vespertilionidae	*Myotis*	*bocagii*	LC							1	
Vespertilionidae	*Myotis*	*tricolor*	LC						1		
Vespertilionidae	*Myotis*	*welwitschii*	LC								1
Vespertilionidae	*Neoromicia*	*anchietae*	LC						1		
Vespertilionidae	*Neoromicia*	*zuluensis*	LC						1		
Vespertilionidae	*Nycticeinops*	*schlieffeni*	LC		1						
Vespertilionidae	*Pipistrellus*	*hesperidus*	LC			1					
Vespertilionidae	*Pipistrellus*	*rusticus*	LC								1
Vespertilionidae	*Scotophilus*	*dinganii*	LC	1	1						
Vespertilionidae	*Scotophilus*	*viridis*	LC						1		

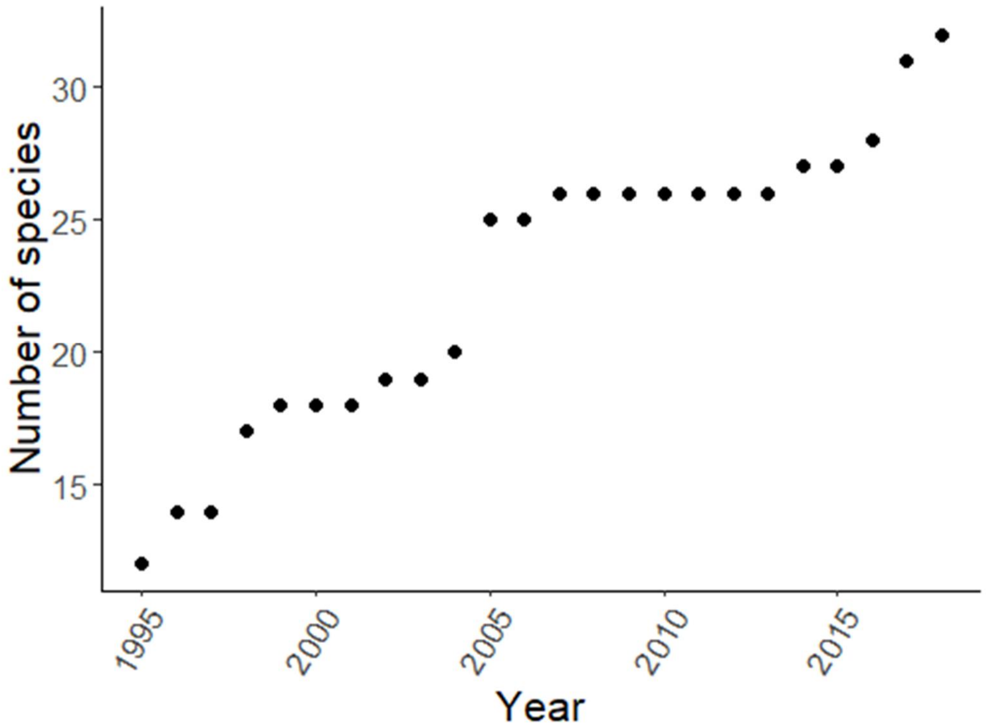

Fig. 3 – Species accumulation curve showing the increase in species richness over time from 1995 to 2018 in Eswatini

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 centre 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 north-east (Fig. 4). There was a strong correlation between species richness and sampling effort ($F = 17900$, $DF = 1022$, $R^2 = 0.946$).

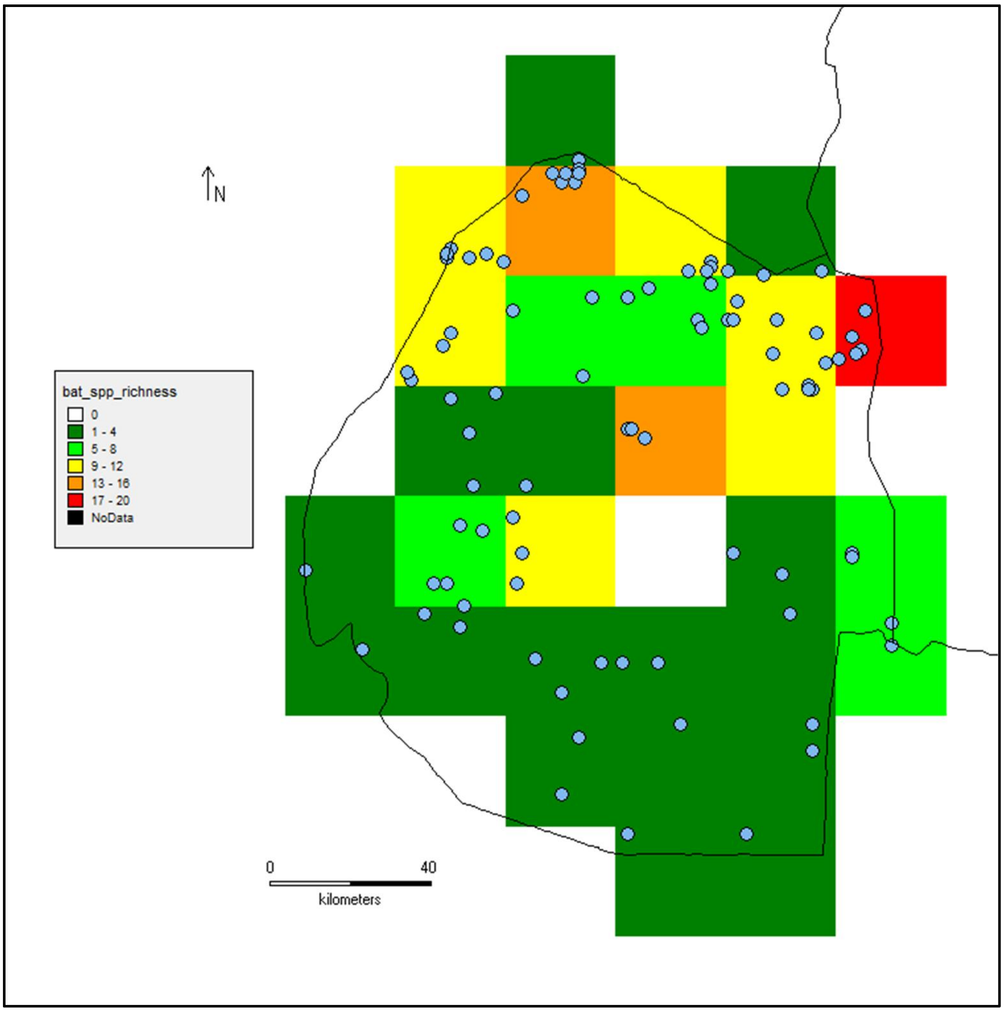

Fig. 4 – The distribution of all bat specimens collected in Eswatini (dots) laid over a “quarter-degree” grid (025° × 025°) showing the number of bat species recorded within each grid

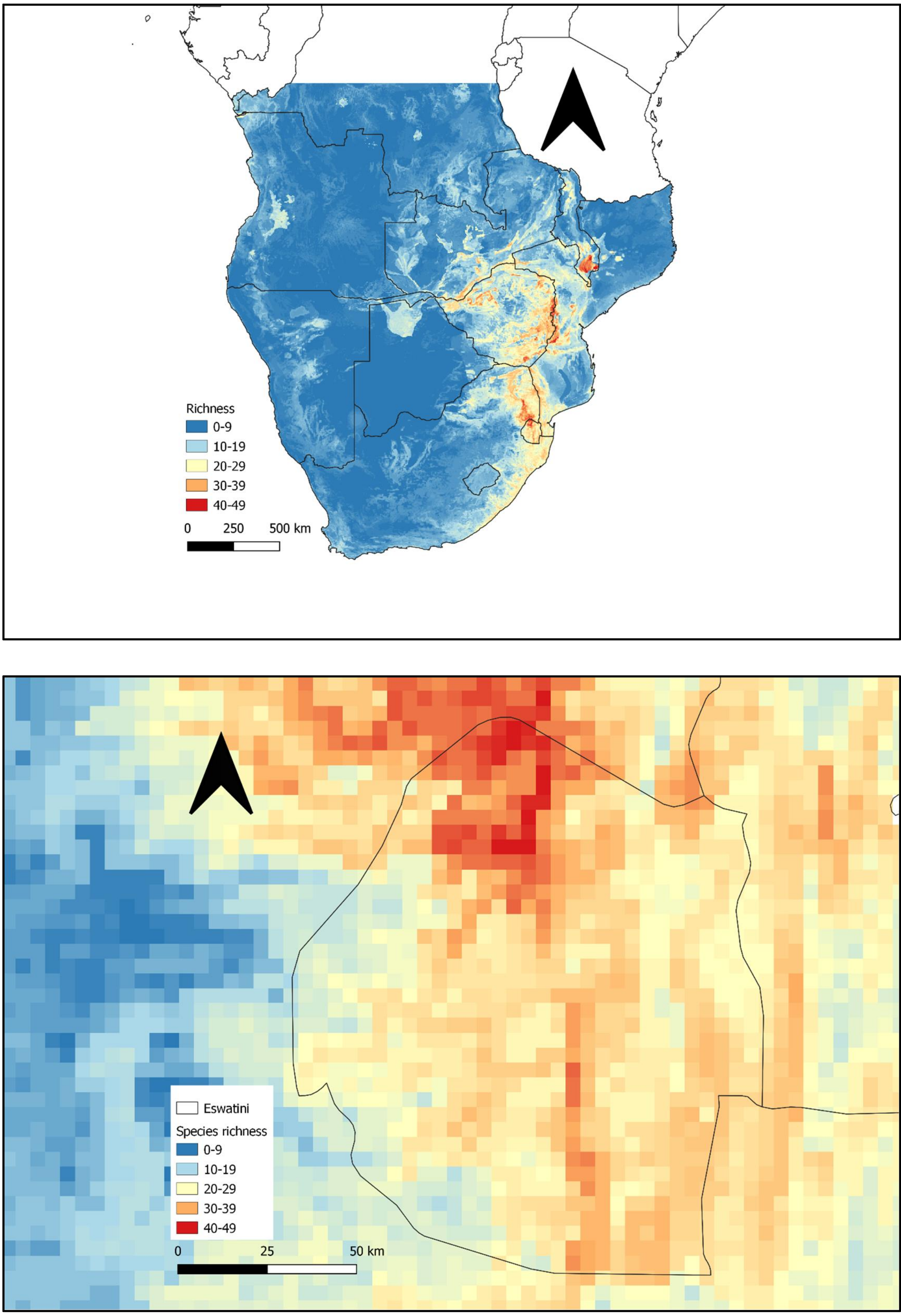

Fig. 5 – Maps showing predicted species richness of bats based on Maxent models: a) for southern Africa as defined in this study (following Monadjem et al. 2020a); and b) for Eswatini. Note that the map presented in (b) is simply a zoomed in section of (a)

However, the modelled 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). Modelled 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 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 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

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

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

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 the probability of occurrence in Eswatini. 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 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, 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 if <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 fifth belonging 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*) 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. 2012, Amori et al. 2012).

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Supplementary material

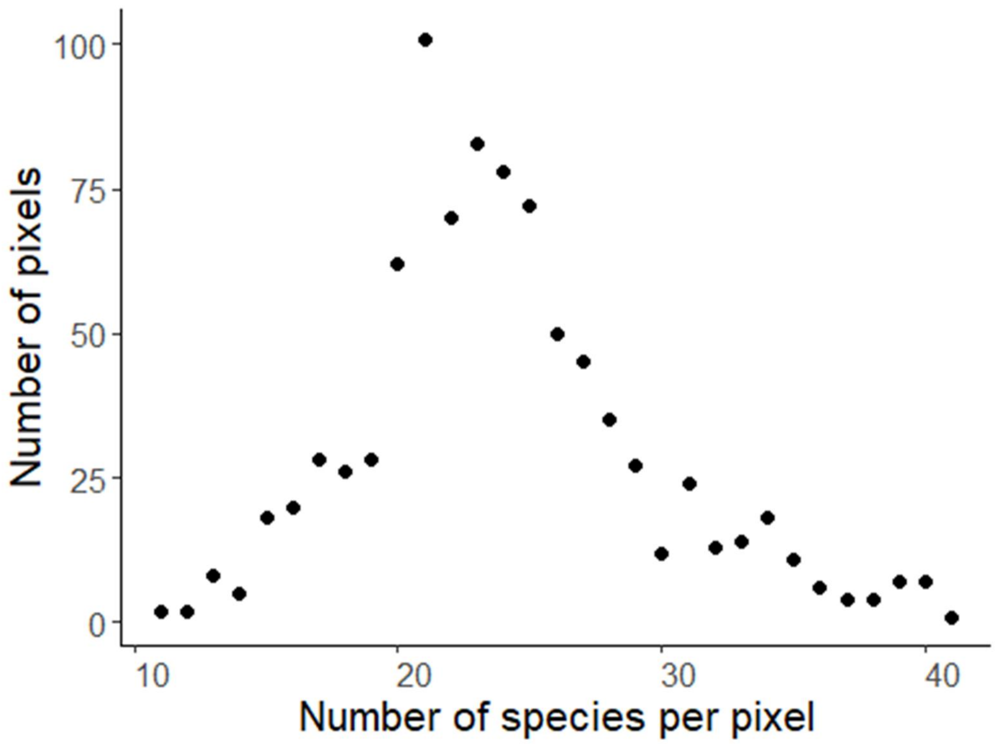

Fig. S1 – A count of the number of bat species per pixels in Eswatini based on Maxent species distribution models, ranging from a minimum of 11 bats per pixel up to a maximum of 41 bats per pixel

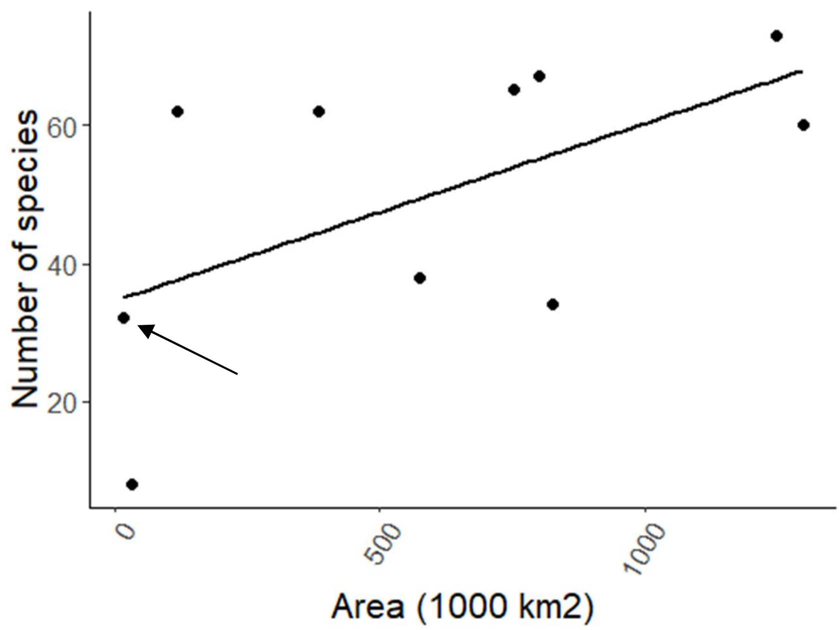

Fig. S2 – A linear regression of species richness against surface area for countries in southern Africa south of the Zambezi-Kunene rivers. The arrow points to Eswatini. Species richness = 0.0000267 *area + 34.25 ($F_{1,8}$ = 392, P = 008318)

Table S1 – The 92 species used in the distribution models, number of occurrence points per species, model performance based on training and test AUC values and the individual contributions (%) of the 13 environmental variables (see Table 1 for a full description of each variable) used in this study. See the Methods for more details.

Species	Total no. of points	AUC (training)	AUC (test)	Altitude	Roughness	BIO2	BIO3	BIO8	BIO9	BIO13	BIO14	BIO15	BIO18	BIO19	Ecoregions
Afronycteris nana	237	0.8532	0.8354	1.2158	7.0918	16.4326	5.1115	1.6581	11.4016	12.8542	5.8932	1.4130	0.8772	0.3387	35.7124
Chaerephon ansorgei	33	0.9452	0.7636	3.8550	19.0007	3.8405	0.0000	0.1178	1.7195	0.2287	1.4951	0.6415	7.8641	3.4871	57.7500
Chaerephon bivittatus	14	0.9612	0.5445	0.9556	19.6017	0.0000	0.0000	0.0000	1.1705	0.0000	1.4648	12.9121	1.5171	11.3189	51.0593
Chaerephon chapini	17	0.9308	0.5131	0.9139	5.5956	1.8443	0.0000	1.5131	0.0000	3.9676	20.1952	0.0000	0.0000	0.6691	65.3012
Chaerephon nigeriae	43	0.9221	0.7796	0.3910	0.8433	5.6236	11.3447	0.0000	0.5892	6.6316	60.0022	0.0000	3.5109	1.1369	9.9266
Chaerephon pumilus	220	0.9303	0.8798	35.6290	2.3288	0.3260	0.6844	1.6550	9.1520	1.5603	3.9001	0.6091	7.9390	0.5834	35.6330
Cistugo lesueuri	19	0.9825	0.8068	28.9366	3.3900	0.0000	0.2051	0.0000	27.9977	0.0000	21.7848	0.0000	0.0000	0.0000	17.6858
Cistugo seabrae	13	0.9937	0.8445	1.4196	14.8602	0.0000	0.0148	1.1552	0.0000	14.9403	1.5762	0.0000	54.6127	4.4628	6.9585
Cloeotis percivali	35	0.9564	0.8870	1.7821	21.6107	6.2103	0.0000	0.0632	22.9375	1.4268	0.0000	0.0000	7.6078	8.0420	30.3197
Eidolon helvum	82	0.8624	0.7060	12.9345	18.2607	1.3297	0.0204	0.1540	2.4906	0.0000	3.6116	0.4624	0.1774	2.3003	58.2584
Epomophorus angolensis	20	0.9726	0.9852	4.5944	4.2278	0.5092	1.3528	0.0000	0.0000	6.1776	33.4143	0.0094	2.8973	2.4099	44.4073
Epomophorus crypturus	113	0.9008	0.8103	0.2702	1.3863	0.0000	12.6318	0.1877	3.6182	19.3685	0.0000	2.4149	2.1421	2.7560	55.2242
Epomophorus dobsonii	30	0.9393	0.8816	4.1088	2.9922	2.3809	1.2891	0.0000	4.0678	34.1131	22.4782	0.0000	0.0000	10.0407	18.5292
Epomophorus labiatus	25	0.9797	0.7978	1.0146	2.5009	14.2655	5.6922	0.0968	2.6638	22.1620	8.0059	0.0000	8.1289	0.4938	34.9757
Epomophorus wahlbergi	176	0.9084	0.8623	3.8243	16.9064	1.4962	1.2361	0.0282	6.4406	0.1478	24.3839	0.1153	14.0915	2.3204	29.0094
Epomops franqueti	12	0.9555	0.7098	0.0000	7.9718	0.2625	0.9954	4.8176	54.0177	0.0000	0.2743	0.0000	6.1448	2.4635	23.0524
Eptesicus hottentotus	50	0.9339	0.7693	4.0785	52.8493	2.5194	0.0000	0.6762	6.8676	0.1278	0.0000	6.2648	0.9092	0.7946	24.9126
Glauconycteris argentata	7	0.9928	0.9998	1.5726	4.9904	0.0000	0.0000	0.0000	19.8852	18.5073	0.0000	0.0000	0.0000	16.6869	38.3576
Glauconycteris variegata	42	0.9238	0.7142	27.4552	0.9681	0.0956	11.1731	0.2627	2.1851	16.2946	9.3796	0.0000	0.7953	2.1700	29.2206
Hipposideros caffer	263	0.8440	0.7949	7.8616	17.7340	0.2198	8.3113	0.7213	9.7156	14.2342	0.2389	0.2926	0.3677	0.0597	40.2433
Hipposideros ruber	37	0.9235	0.7582	0.0000	24.0274	7.3054	0.7577	0.0000	0.1329	51.1290	1.0131	0.0000	1.9979	7.3687	6.2678
Hypsignathus monstrosus	10	0.9829	0.9801	1.6269	19.9407	14.0432	0.0000	0.0000	27.4990	0.0000	0.0000	0.0000	13.3006	1.1572	22.4322
Kerivoula argentata	32	0.9493	0.6996	11.0618	6.6313	4.5121	3.6130	0.0000	0.0694	19.0043	11.5596	0.0626	3.0510	3.1440	37.2910
Kerivoula lanosa	31	0.9462	0.8545	0.2771	7.4098	0.0186	2.4834	0.9574	5.8713	1.3039	25.9882	0.0000	0.5044	0.4735	54.7124
Laephotis angolensis	6	0.9767	0.9375	0.0314	7.1930	0.9708	0.0000	0.0000	0.0000	16.8448	29.4669	0.0000	0.3131	6.6266	38.5534
Laephotis botswanae	37	0.9498	0.8231	0.8497	9.8305	0.6596	0.3023	0.0000	11.8609	7.6325	1.5413	0.7878	0.7207	0.8353	64.9794

Laephotis capensis	395	0.8415	0.8149	0.9225	5.0193	0.9398	3.5643	0.4605	28.1680	8.5279	10.8716	0.5138	3.0426	2.5063	35.4633
Laephotis stanleyi	14	0.9746	0.8354	0.0000	1.3885	2.1490	0.0000	2.2054	0.0000	0.0000	0.0000	0.6607	0.0000	15.9191	77.6774
Lavia frons	11	0.9777	0.8693	0.0000	2.1792	4.4226	0.1132	0.0000	32.1124	0.2672	9.2142	0.0000	0.0032	1.5024	50.1856
Macronycteris vittatus	84	0.8848	0.8469	0.1212	5.1241	1.6971	0.1409	0.0043	5.5559	22.4094	0.0000	26.2942	0.3016	2.3469	36.0045
Micropteropus pusillus	25	0.9576	0.8944	4.1369	6.0705	43.7518	0.5642	0.1036	11.8362	4.6980	0.2943	0.0000	7.8168	0.5598	20.1678
Mimetillus thomasi	13	0.8929	0.7340	0.2539	0.0674	17.0389	0.7319	0.0000	3.5222	44.7014	15.8144	0.0000	0.0000	4.3403	13.5296
Miniopterus cf natalensis	55	0.9372	0.8350	2.0445	5.4847	13.9829	10.3590	0.0000	2.0779	14.2389	0.0186	0.0000	5.5497	4.1043	42.1395
Miniopterus fraterculus	21	0.9953	0.9400	1.0821	17.3542	0.1048	0.0000	0.0000	6.9451	0.0000	40.9233	0.0000	11.1223	0.0000	22.4683
Miniopterus inflatus	20	0.9705	0.5760	1.5403	19.5136	0.7918	12.5234	0.0000	2.3230	4.6542	11.7527	0.0000	0.2823	8.2144	38.4042
Miniopterus minor	6	0.9845	0.7443	0.0000	26.7413	0.0000	0.0000	0.0000	0.0000	10.4897	34.5850	0.0000	1.3585	0.0000	26.8256
Miniopterus mossambicus	12	0.9945	0.8640	0.0000	28.0162	0.0000	0.0000	0.0790	1.8782	10.3093	29.8142	4.7041	13.3038	0.0000	11.8952
Miniopterus natalensis	182	0.9019	0.8784	3.4869	25.5127	0.2111	0.6353	0.0355	27.6593	8.1720	18.9091	0.0054	2.5438	0.7823	12.0466
Mops condylurus	112	0.9249	0.9327	36.5604	0.2296	1.6518	4.5063	2.8873	5.1039	8.3060	1.2671	0.1023	0.4459	0.0008	38.9387
Mops midas	36	0.9550	0.9261	2.9678	0.0498	2.7724	0.0108	16.1316	17.9252	0.1692	0.0518	0.3173	0.0013	0.3963	59.2064
Mops niveiventer	21	0.9703	0.7983	4.6054	5.2521	10.5126	1.3231	0.0000	0.1360	37.0715	5.4996	0.1160	0.5566	2.0858	32.8414
Myonycteris angolensis	17	0.9601	0.9708	0.0630	28.5964	0.4917	9.4142	0.0000	0.0000	0.0000	10.4808	1.8088	24.0523	4.7958	20.2969
Myonycteris goliath	7	0.9935	0.9819	0.0000	40.2764	0.0000	0.0243	0.0000	0.1658	0.0000	33.2158	8.0430	9.5458	0.0000	8.7290
Myotis bocagii	49	0.9032	0.7447	3.5968	23.7465	2.4614	0.0000	0.2623	3.4616	17.1170	0.0000	3.3546	2.8541	0.1632	42.9823
Myotis tricolor	71	0.9433	0.9562	1.6686	37.7972	0.8220	6.4332	0.0000	6.5687	0.0105	28.4150	0.2689	6.0518	2.2966	9.6677
Myotis welwitschii	35	0.9231	0.7658	0.0000	27.0073	1.6154	4.7562	0.0000	9.2968	10.5779	8.3692	7.2023	7.0558	11.7712	12.3480
Neoromicia anchietae	56	0.9462	0.8370	9.8689	3.9541	2.5035	0.0026	0.0000	19.6384	16.8214	0.0000	0.0000	0.2198	0.0988	46.8927
Neoromicia zuluensis	96	0.9034	0.8602	2.7323	7.6224	1.4583	1.6595	2.9758	16.8252	5.7586	0.0000	1.8101	2.1305	2.3172	54.7101
Nycteris grandis	15	0.9794	0.8348	29.6898	0.0089	0.0000	0.5515	1.0059	0.0043	5.5871	0.0000	0.0000	0.0706	9.2506	53.8313
Nycteris hispida	54	0.8918	0.8156	5.0432	3.6519	5.1881	0.1465	3.4084	2.9733	41.9111	7.0944	0.6973	0.2657	0.0962	29.5239
Nycteris macrotis	56	0.8901	0.7554	0.6626	3.4212	7.7364	0.0000	1.1729	0.0156	31.4818	0.0000	0.7033	3.6153	6.2222	44.9687
Nycteris thebaica	363	0.8097	0.8013	4.3870	12.9899	1.9347	27.4229	0.0814	6.7169	3.8348	0.0000	0.0589	0.6264	0.0000	41.9471
Nycteris woodi	25	0.9650	0.8781	2.0335	1.8798	0.0000	0.9470	0.4850	0.5055	1.0161	7.7741	0.3259	0.7296	4.0066	80.2969
Nycticeinops grandidieri	9	0.9758	0.7774	0.0000	8.2784	0.0000	0.5292	0.0000	0.7706	45.3365	11.6686	0.1254	0.0000	7.2432	26.0481
Nycticeinops schlieffeni	152	0.9255	0.8549	2.7654	4.9391	3.9315	7.0776	3.8613	7.2623	8.8766	0.0000	0.1786	1.2659	1.4342	58.4075
Otomops martiensseni	16	0.9950	0.7687	10.9056	15.5538	2.3339	1.5572	1.0921	3.9213	1.6908	0.0000	0.0000	0.0000	0.5571	62.3883
Pipistrellus hesperidus	74	0.9597	0.8685	2.3366	7.3454	0.0000	1.1846	0.2715	14.0020	10.9063	30.0142	0.0321	0.2449	3.9183	29.7442
Pipistrellus rusticus	58	0.9348	0.8794	0.0365	3.3261	3.4176	8.9899	3.9811	12.5936	13.9069	0.0000	1.8814	0.0000	0.3192	51.5478
Plerotes anchietae	10	0.9822	0.9927	26.5799	28.8237	0.0000	0.0000	0.3156	0.0176	19.1584	13.1813	0.0000	0.4905	3.0552	8.3778
Pseudoromicia rendalli	14	0.9606	0.7776	32.2637	0.0000	0.0000	0.0299	7.2714	0.0000	0.6096	0.0000	1.3704	0.0000	2.3077	56.1473
Pseudoromicia tenuipinnis	14	0.9730	0.8159	0.3173	0.1697	0.0000	2.7283	0.0000	41.0438	0.0000	0.6371	0.0035	5.3097	0.1805	49.6100
Rhinolophus blasii	46	0.9585	0.9394	0.0000	25.7082	0.4710	7.4229	0.0000	6.2197	17.4104	8.0682	3.4832	0.2859	3.1231	27.8074
Rhinolophus capensis	23	0.9964	0.9432	2.1479	1.1290	0.2134	0.3257	14.5860	0.0000	0.0047	0.1218	19.6917	1.5030	53.6176	6.6594
Rhinolophus cf lobatus	24	0.9728	0.8775	0.0000	12.4794	0.4596	0.0000	0.0000	1.2886	6.5792	0.0000	5.7057	0.9012	28.0060	44.5803

Rhinolophus cf mossambicus	19	0.9892	0.8490	1.2832	19.0425	0.0000	0.0000	0.0000	0.0000	0.0000	13.4920	0.4782	7.6000	1.6361	56.4680
Rhinolophus clivosus	197	0.9394	0.9091	0.9097	33.1864	1.0386	11.6198	8.3045	6.5032	3.2384	21.3214	0.1233	1.7769	0.1975	11.7805
Rhinolophus cohenae	6	0.9974	0.9946	0.0000	41.7889	0.0000	0.0000	0.0000	4.5746	0.0000	20.7921	0.0000	7.0924	0.2180	25.5340
Rhinolophus damarensis	39	0.9830	0.7128	10.0760	23.1949	0.5354	2.1802	0.0000	1.3450	21.2377	2.9865	1.6850	6.9147	3.7669	26.0777
Rhinolophus darlingi	103	0.9473	0.9318	0.8018	1.7941	4.4229	2.5362	0.0437	18.5562	0.4994	7.6533	0.0892	10.2271	0.8123	52.5640
Rhinolophus denti	19	0.9766	0.8949	0.0000	12.5557	9.7070	0.5099	0.0000	5.5230	2.3581	3.2699	0.0000	0.4380	0.2733	65.3652
Rhinolophus fumigatus	88	0.9373	0.7678	3.4506	27.5310	0.1970	3.0786	0.4679	5.3982	6.4739	5.7233	20.3085	0.5116	0.3033	26.5560
Rhinolophus lobatus	38	0.9588	0.8916	17.5468	0.0502	0.6370	1.6244	0.9505	0.7766	2.2627	0.0000	5.5399	0.0000	1.9773	68.6346
Rhinolophus mossambicus	119	0.9415	0.9433	0.9509	2.1741	3.0885	4.3495	0.0315	3.6046	14.5547	1.0594	13.1240	0.7391	0.2175	56.1062
Rhinolophus rhodesiae	43	0.9316	0.9169	0.0674	22.0597	4.3406	2.0565	0.4933	6.6218	15.3545	0.0000	1.8654	0.0000	0.7488	46.3920
Rhinolophus simulator	100	0.9414	0.9208	0.1590	18.2124	0.2207	16.6466	0.1365	16.8073	1.6791	5.2029	0.1603	20.2972	5.2596	15.2183
Rhinolophus smithersi	18	0.9929	0.9438	0.0000	15.5716	0.0000	0.0000	8.0517	10.3298	0.0000	9.4055	3.6980	0.7465	0.6702	51.5266
Rhinolophus swinnyi	8	0.9945	0.9971	0.2351	4.4765	2.6788	0.0000	0.0000	0.1818	0.0000	52.4311	0.0000	0.0000	0.0000	39.9968
Rousettus aegyptiacus	72	0.9138	0.8508	3.6178	31.1238	7.2709	7.4403	0.0000	6.1326	0.1772	22.2451	0.3421	3.0725	0.5288	18.0489
Sauromys petrophilus	63	0.9508	0.9248	0.4871	19.7270	3.7609	1.6278	0.5912	0.7925	33.7671	5.0069	5.3328	0.5012	3.1004	25.3050
Scotoecus albofuscus	7	0.9923	0.1066	57.7109	0.0204	0.0002	10.9834	0.0000	0.0000	0.0201	0.0000	0.0000	3.1984	3.7786	24.2881
Scotoecus hindei	23	0.9410	0.7052	5.1046	0.0500	0.0000	0.5918	0.0000	6.1618	20.2896	1.3124	0.0000	0.0573	0.7360	65.6965
Scotophilus alvenslebeni	6	0.9800	0.4529	44.3817	4.0470	0.0000	1.5088	0.0000	0.0000	0.0000	33.4946	0.0000	0.2059	0.0000	16.3620
Scotophilus dinganii	253	0.8667	0.8316	0.2909	4.9376	0.0464	2.9012	0.4727	20.1849	21.5715	7.1407	0.0143	0.1937	1.1306	41.1153
Scotophilus leucogaster	43	0.9444	0.8469	1.5794	13.5365	2.9127	0.1303	11.6024	7.9976	7.3935	12.5666	0.3096	1.8729	2.8650	37.2334
Scotophilus viridis	70	0.9432	0.8794	30.8308	2.5353	1.6851	9.8745	1.7311	4.6900	9.5083	0.0000	0.1188	0.0621	0.4414	38.5227
Tadarida aegyptiaca	175	0.8723	0.8092	0.8204	18.2536	2.5798	0.1574	2.9773	33.1609	3.8100	15.9902	0.1118	0.0958	0.0166	22.0263
Tadarida fulminans	19	0.9755	0.8211	0.1417	18.9670	0.0000	0.3375	0.0000	2.3951	2.1672	0.0000	16.3531	0.0000	16.0606	43.5778
Tadarida ventralis	9	0.9521	0.7656	0.0000	25.7713	0.0000	1.9103	0.0000	0.0000	6.2509	14.5104	4.7180	0.0000	0.0807	46.7584
Taphozous mauritianus	112	0.8415	0.7121	0.0234	1.5968	3.2110	0.7562	0.2448	0.8680	10.5668	0.0537	0.0000	4.6840	1.9270	76.0682
Taphozous perforatus	12	0.9498	0.4923	0.2108	1.9345	0.0000	0.0000	0.0000	4.8265	6.0352	9.5845	0.8747	1.7831	0.0000	74.7508
Triaenops afer	14	0.9736	0.8391	36.5579	5.2068	0.1397	0.0000	2.6036	0.0864	8.4952	0.0000	5.7682	0.3530	2.8360	37.9532
Vansonia rueppellii	42	0.8869	0.6934	0.0000	1.1738	0.0005	0.0000	2.7298	0.3157	0.2550	3.8797	13.7422	0.0035	4.5679	73.3319

Table S2 – Bat species predicted (n = 47) and recorded to date (n = 32) to occur in Eswatini based on species distribution models and museum specimens, respectively

Family	Genus	Species	Predicted	Recorded
Pteropodidae	*Eidolon*	*helvum*	1	
Pteropodidae	*Epomophorus*	*crypturus*	1	1
Pteropodidae	*Epomophorus*	*wahlbergi*	1	1
Pteropodidae	*Rousettus*	*aegyptiacus*	1	
Hipposideridae	*Hipposideros*	*caffer*	1	1
Rhinonycteridae	*Cloeotis*	*percivali*	1	1
Rhinolophidae	*Rhinolophus*	*blasii*	1	1
Rhinolophidae	*Rhinolophus*	*clivosus*	1	1
Rhinolophidae	*Rhinolophus*	*cohenae*	1	
Rhinolophidae	*Rhinolophus*	*darlingi*	1	1
Rhinolophidae	*Rhinolophus*	*rhodesiae*	1	1
Rhinolophidae	*Rhinolophus*	*simulator*	1	1
Rhinolophidae	*Rhinolophus*	*smithersi*	1	
Emballonuridae	*Taphozous*	*mauritianus*	1	1
Emballonuridae	*Taphozous*	*perforatus*	1	
Nycteridae	*Nycteris*	*macrotis*	1	
Nycteridae	*Nycteris*	*thebaica*	1	1
Molossidae	*Chaerephon*	*ansorgei*	1	
Molossidae	*Chaerephon*	*pumilus*	1	1
Molossidae	*Mops*	*condylurus*	1	1
Molossidae	*Mops*	*midas*	1	1
Molossidae	*Otomops*	*martiensseni*	1	
Molossidae	*Tadarida*	*aegyptiaca*	1	1
Miniopteridae	*Miniopterus*	*fraterculus*	1	1
Miniopteridae	*Miniopterus*	*inflatus*	1	

Miniopteridae	*Miniopterus*	*natalensis*	1	1
Miniopteridae	*Miniopterus*	*mossambicus*	1	
Vespertilionidae	*Afronycteris*	*nana*	1	1
Vespertilionidae	*Eptesicus*	*hottentotus*	1	1
Vespertilionidae	*Laephotis*	*botswanae*	1	
Vespertilionidae	*Laephotis*	*capensis*	1	1
Vespertilionidae	*Kerivoula*	*argentata*	1	1
Vespertilionidae	*Kerivoula*	*lanosa*	1	1
Vespertilionidae	*Myotis*	*bocagii*	1	1
Vespertilionidae	*Myotis*	*tricolor*	1	1
Vespertilionidae	*Myotis*	*welwitschii*	1	1
Vespertilionidae	*Neoromicia*	*anchietae*	1	1
Vespertilionidae	*Neoromicia*	*zuluensis*	1	1
Vespertilionidae	*Nycticeinops*	*grandidieri*	1	
Vespertilionidae	*Nycticeinops*	*schlieffeni*	1	1
Vespertilionidae	*Pipistrellus*	*hesperidus*	1	1
Vespertilionidae	*Pipistrellus*	*rusticus*	1	1
Vespertilionidae	*Pseudoromicia*	*rendalli*	1	
Vespertilionidae	*Scotoecus*	*albofuscus*	1	
Vespertilionidae	*Scotoecus*	*hindei*	1	
Vespertilionidae	*Scotophilus*	*dinganii*	1	1
Vespertilionidae	*Scotophilus*	*viridis*	1	1

Table S3 – The five new species recorded in Eswatini since the publication of last bat checklist for the country by Shapiro and Monadjem (2016), together with additional information on the collecting localities and number of individuals captured

Family, Species	Locality	Latitude	Longitude	Elevation (m)	Number of individuals captured
Rhinolophidae, *Rhinolophus rhodesiae*	Bulembu	-25.95977	31.11844	1210	2
Vespertilionidae, *Eptesicus hottentotus*	Ntfungula	-26.75476	31.16174	1200	1
Vespertilionidae, *Kerivoula argentata*	Mambane	-26.83912	32.13247	60	1
Vespertilionidae, *Myotis welwitschii*	Dombeya Game Reserve	-26.36068	31.5447	440	1
Vespertilionidae, *Pipistrellus rusticus*	Mvembili	-25.75719	31.41769	470	10
	Sigcineni	-26.69995	31.28313	430	3
	Velezizweni	-26.70120	31.11966	910	1