



features contribute to increase landscape heterogeneity and promote bat diversity providing roosting sites and/or suitable foraging habitat.

### Functional groups and habitat selection in bats

Bat species can be divided into three functional groups based on foraging niche (Schnitzler and Kalko, 2001; Monadjem et al., 2010; Denzinger and Schnitzler, 2013): open air foragers, background clutter (edge) foragers, and clutter foragers. This subdivision is based on the adaptive complex between wing morphology and echolocation (Aldridge and Rautenbach, 1987; Norberg and Rayner, 1987; Arita and Fenton, 1997) that broadly define where a bat roosts and forages, hence determining the habitat that can be selected. Open air foragers have long, narrow wings (typical of, for example, the Molossidae) that are capable of fast flight but with low manoeuvrability and therefore tend to forage in open, uncluttered environments such as above the canopy of the vegetation. Furthermore, they usually emit low frequency echolocation pulses of long duration that can travel long distances thus allowing the detection of prey insects even when in fast flight. These bats tend to select roosts, such as crevices (e.g. *Sauromys petrophilus*) or anthropogenic structures (e.g. *Tadarida aegyptiaca*), that allow them to commence flight without encountering obstacles (Monadjem et al., 2010). In contrast, clutter foraging bats have short, broad wings (typical of Pteropodidae and Rhinolophidae) that have sacrificed speed for manoeuvrability and are therefore capable of foraging in cluttered environments such as within dense vegetation. Furthermore, echolocation calls involve either high duty-cycle with a constant frequency component (Rhinolophidae and Hipposideridae), or steep frequency modulation (Vespertilionidae) which allows fine-scale discrimination of objects as would be encountered in a cluttered environment. As a result, these species can roost, for example, in trees or other cluttered environments (Monadjem et al., 2010). Background clutter foragers present a mix of these features and can often exploit a wide range of habitats intermediate between open air and cluttered environments.

In the arid region considered, community guild composition will be affected by the habitat available, and competition between sympatric species might be heightened by the scarcity of resources, particularly in terms of roosting sites and food availability.

### The arid region of southern Africa

Southern Africa experiences a strong climatic gradient, with rainfall increasing from west to east and seasonality of precipitation switching from winter rainfall in the south-west to summer rainfall in the east and north (Rutherford and Westfall, 1986; Rutherford et al., 2006). As a result, a diverse set of habitats occur in this region, leading to high species richness across taxa, including the bat fauna (Monadjem et al., 2010). Yet diversity patterns vary largely within southern Africa (Schoeman et al., 2013). In this paper we focus on the bats of the arid and semi-arid zones (from now on referred to as the “arid region”), located in the south-west of southern Africa, and in particular on those areas receiving less than 250 mm and that are considered to be deserts and semi-deserts (Rutherford et al., 2006).

The arid region spans three southern African countries, namely Namibia, Botswana and South Africa, and it consists of four major ecological zones, the Namib Desert, the Succulent Karoo, the Nama Karoo and the Kalahari “Desert”. The Namib Desert, a long and narrow strip of aridity, lies in the extreme west, wedged between the Atlantic Ocean and the escarpment. To the south of the Namib, but still along the Atlantic coast, lies the Succulent Karoo. The Nama Karoo occurs to the east of the Namib and Succulent Karoo. To the north of the Nama Karoo lies the vast Kalahari “Desert”. These four zones constitute different ecosystems, defined primarily by precipitation patterns. The annual precipitation and the approximate boundaries of these four regions are illustrated in Fig. 1. The Namib Desert is the driest region receiving 15–70 mm of rain annually, followed by the Succulent Karoo with 20–290 mm, the Nama Karoo with 100–500 mm, and the Kalahari with 200–300 mm (Rutherford and Westfall, 1986). It should be noted that three of these zones (i.e. Namib Desert, Succulent Karoo

and Nama Karoo) are recognised as separate biomes (Rutherford and Westfall, 1986), whereas the Kalahari, on account of its relatively high annual rainfall, is not considered a true desert, but rather an extremely dry savannah developed on Kalahari sands. As a consequence of this peculiarity, it harbours distinct vegetation associations (see Mucina and Rutherford, 2006).

### Methods

To describe patterns of species diversity within the arid region based on reported records, bat distributions were extracted from Monadjem et al. (2010). All bat records falling within the arid region as described in Fig. 1 were included. Using this dataset we calculated bat species richness for each zone and discussed patterns in light of zone-specific environmental factors.

Additionally, to overcome possible biases caused by unequal sampling effort across southern Africa, we discuss richness patterns obtained by modelling potential distributions of 208 species of bats occurring in sub-Saharan Africa. Since the development of the species richness map for African bats falls partly out of the scope of this study, methods applied in its development are reported in detail in Appendix S1.

We compared the size, wing morphology and echolocation of bats from four different arid regions around the world to elucidate differences in functional diversity of bats among them. The four regions are: 1) the southern African arid; 2) the Negev Desert, Israel (Korine and Pinshow, 2004; Razgour, 2008; Razgour et al., 2011); 3) the arid region of Australia (Morton, 1979; McKenzie et al., 2002; McKenzie and Bullen, 2003; Williams and Dickman, 2004); and south-western North America (Morton, 1979; Norberg and Rayner, 1987; O’Farrell et al., 1999). For each bat species, we recorded the following descriptive variables: roost type (cave, crevice or tree); diet (insectivore, frugivore, carnivore or nectivore); and functional group (open air, edge or clutter). Furthermore, we also recorded the mean mass, wingloading, aspect ratio and peak frequency of each species (from Norberg and Rayner, 1987 and Aldridge and Rautenbach, 1987). We chose these parameters because there are strong correlations between habitat use and these variables (Aldridge and Rautenbach, 1987). A principal components analysis (PCA) of the above measurements was conducted on the variance–covariance matrix in the program PAST (Hammer et al., 2001) to compare the ecomorphology of bats in the four arid regions.

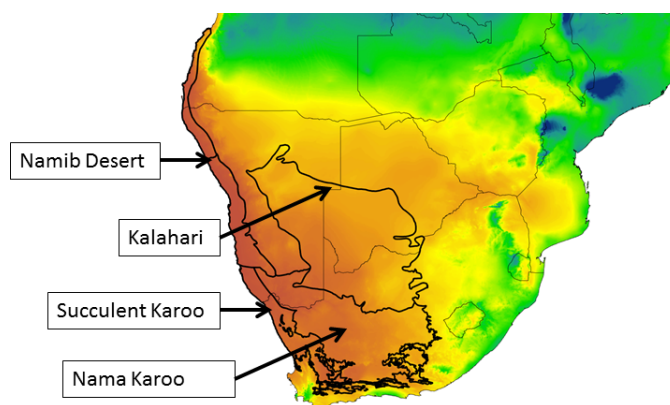


Figure 1 – Map showing the distribution of the four arid zones in southern Africa. Annual precipitation is also shown (dark brown – lowest rainfall, dark blue – highest rainfall).

## Results and discussion

### Patterns of bat species richness in the arid region of southern Africa

#### Bat species richness

A total of 17 species (see Tab. 1), belonging to eight families of bats, are known to occur in the southern African arid region, and an additional

**Table 1** – The bat species recorded in the arid region of southern Africa (based on Smithers, 1971; Stuart, 1975; Nel et al., 1984; Heselmann and Norton, 1985; Monadjem et al., 2010) and their current IUCN status (IUCN, 2017), with NT indicating Near Threatened and LC Least Concern species. Bats have been recorded as resident (Res), absent (Abs), vagrant (Vag) or marginal (Mar) with respect to the area of interest.

Family and species	Kalahari	Namib	Succulent Karoo	Nama Karoo	IUCN status
<b>Pteropodidae</b>					
<i>Eidolon helvum</i>	Vag	Vag	Abs	Abs	NT
<b>Hipposideridae</b>					
<i>Hipposideros caffer</i>	Abs	Mar	Abs	Mar	LC
<b>Rhinolophidae</b>					
<i>Rhinolophus capensis</i>	Abs	Res	Res	Abs	LC
<i>Rhinolophus clivosus</i>	Mar	Abs	Res	Res	LC
<i>Rhinolophus damarensis</i>	Mar	Res	Res	Res	LC
<i>Rhinolophus denti</i>	Res	Abs	Abs	Res	LC
<i>Rhinolophus fumigatus</i>	Abs	Mar	Abs	Abs	LC
<b>Nycteridae</b>					
<i>Nycteris thebaica</i>	Res	Res	Res	Res	LC
<b>Molossidae</b>					
<i>Sauromys petrophilus</i>	Abs	Res	Res	Abs	LC
<i>Tadarida aegyptiaca</i>	Res	Res	Res	Res	LC
<b>Miniopteridae</b>					
<i>Miniopterus natalensis</i>	Mar	Res	Res	Res	LC
<b>Cistugidae</b>					
<i>Cistugo seabrae</i>	Abs	Res	Mar	Res	LC
<b>Vespertilionidae</b>					
<i>Eptesicus hottentotus</i>	Mar	Res	Res	Res	LC
<i>Laephotis namibensis</i>	Abs	Res	Res	Abs	LC
<i>Neoromicia capensis</i>	Res	Res	Res	Res	LC
<i>Neoromicia zuluensis</i>	Abs	Res	Abs	Abs	LC
<i>Pipistrellus rueppellii</i>	Abs	Abs	Abs	Mar?	LC

family (Emballonuridae) may occur marginally at the fringes of this region. The Pteropodidae is only represented by a single vagrant species (*Eidolon helvum*). The families Hipposideridae, Nycteridae, Miniopteridae and Cistugidae are each represented by a single species. The Molossidae accounts for two species, Rhinolophidae for five species and Vespertilionidae for six. Hence, eight out of the ten families of bats occurring southern Africa are represented in this arid region.

Three bat species are endemic or near-endemic to the southern African arid region: *Rhinolophus denti*, *Cistugo seabrae*, and *Laephotis namibensis*. *Rhinolophus denti* occurs in two widely separated geographic populations (and recognized as two different subspecies); one subspecies (*R. d. denti*) is centred on the arid region of southern Africa, while the other one (*R. d. knorri*) occurs thousands of kilometres away in West Africa. It is possible that these two populations represent valid species, which would make *R. d. denti* a near-endemic to the southern African arid region (Monadjem et al., 2010). The other two species have distributions that are tied to the Namib Desert, marginally extending into arid areas adjacent to this true desert. With the exception of *Rhinolophus capensis*, which is endemic to South Africa, the remaining species occur widely in southern Africa, many ranging beyond the sub-region into East and West Africa. Therefore, the level of endemism (3 out of 17 species) is relatively low for arid southern Africa, most species in fact spilling over from the surrounding more humid savannahs. None of the bats occurring in the arid region is listed as globally threatened, with the vagrant *Eidolon helvum* (not included in any of the subsequent analyses) listed as Near Threatened (Tab. 1).

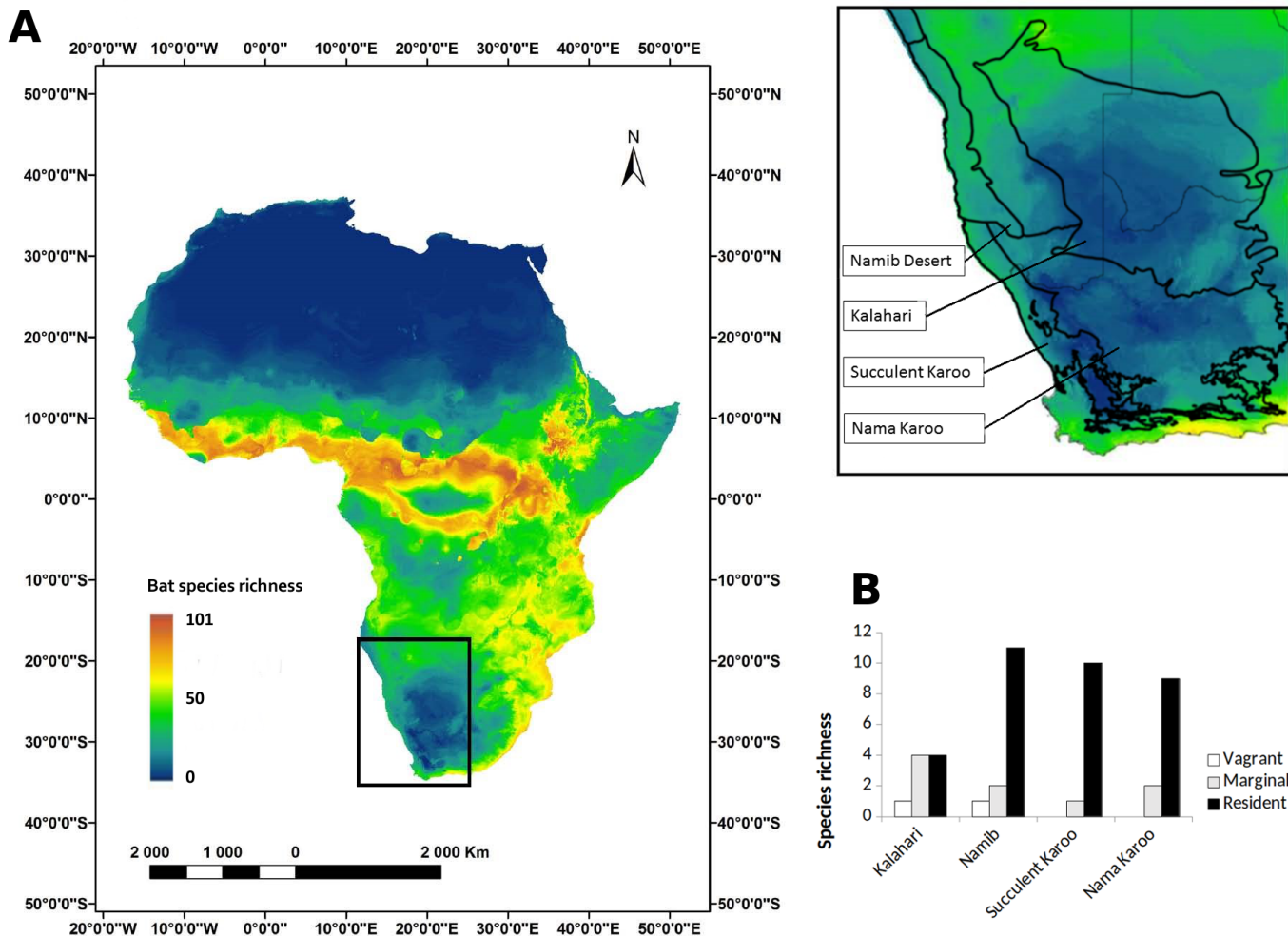
A few other species occur only at the margins of the arid region and, therefore, have not been included in Tab. 1. Among these, a number of woodland species, such as *Chaerephon pumilus*, *Taphozous mauritanus* and *Epomophorus crypturus*, reach the edge of the Kalahari in the Okavango Delta, but do not occur further south in waterless landscapes. The diversity of bats within the southern African arid region is therefore highly impoverished when compared with that

of the savannahs to the east and north. A total of 116 species of bats have been recorded for southern Africa, south of the 5<sup>th</sup> parallel (Monadjem et al., 2010) of which just 15% occur in the arid region. Alpha diversity (i.e. the number of species co-occurring together at one location) in the eastern savannahs of southern Africa regularly exceeds 20 species, whereas in the arid region it is usually around 5 species or less (Schoeman et al., 2013). For example, just three species of bats have been recorded from the Kgalagadi National Park (previously the Kalahari Gemsbok National Park) (Rautenbach, 1971), and eight species from the Namib-Naukluft National Park (Stuart, 1975). Given that both these parks cover vast areas, alpha diversity is probably lower than the values quoted for the parks as a whole.

### Biogeographic patterns of species richness

Distribution of bat species richness in southern Africa has been previously discussed by a number of different authors (Andrews and O'Brien, 2000; Schoeman et al., 2013; Herkt et al., 2016; Cooper-Bohannon et al., 2016). These studies agree in identifying a clear decline in richness from east to west, with greatest species richness in the savannahs of north-eastern South Africa and Zimbabwe, and lowest richness in the arid region of western South Africa, south-western Botswana and southern Namibia (Andrews and O'Brien, 2000; Schoeman et al., 2013; Cooper-Bohannon et al., 2016). However, this pattern varied across bat families and no single environmental variable was identified to explain this pattern. This gradient in species richness closely follows the aridity gradient, with rainfall decreasing from east to west, and it is captured by maps modelling bat species richness in Africa (see Fig. 2A, Appendix S1, and also Herkt et al., 2016). However, the arid region here considered, being a mosaic of different biomes, is highly heterogeneous and requires a more detailed examination in order to understand the pattern of species richness. When looking at the number of species recorded in each of the four zones (see Fig. 2B), it is evident that the species richness in the Kalahari is extremely low, with just four species regularly occurring there, and a further four species occurring marginally, mostly on its southern edge (see Tab. 1 for species identities). This contrasts strongly with the Namib Desert which, although more arid than the Kalahari, has 11 resident species and a further two that occur marginally. The reason for the low species richness in the Kalahari is probably associated with the limited availability of roosting sites: the Kalahari is relatively flat and without caves or cliffs. Additionally, trees are sparsely distributed and mostly occur along drainage lines (such as along the Kuiseb riverbed) (Rautenbach, 1971; Nel et al., 1984). By contrast, the Namib Desert is situated alongside an escarpment where cliffs and small overhangs abound and caves may be present, providing suitable roosts for a number of species (Coetzee, 1969). On the other hand, both the Succulent and Nama Karoo biomes have caves and some cliff sites (e.g. Monadjem et al., 2008; Cooper-Bohannon et al., 2016), and species richness is also higher than that of the Kalahari.

The differences in local richness between the Namib and the Kalahari are interesting since the former is more arid than the latter. This is because at a regional scale species richness is mostly driven by aridity patterns (Andrews and O'Brien, 2000), and therefore we would then expect the Kalahari to have higher species richness. However, on a more local scale other factors, such as habitat heterogeneity and roost availability, might have greater influence. We suggest that bat species occurring across the southern African arid region show sufficient adaptations to water stress, and hence landscape features (such as habitat heterogeneity) may play a larger role than aridity in explaining the presence or absence of species. Factors limiting the presence of bats and their ability to cope with water stress are topics that require further investigation. Interestingly, the contrast in species richness between these two zones (depicted in Fig. 2A) is not reported in Herkt et al. (2016). In the latter study, the Namib Desert is pictured as the least diverse zone of southern Africa, despite the authors accounting for vegetation structure and landscape roughness when modelling potential species ranges across Africa. This illustrates the importance of “ground-validating” species distribution models (Rebelo and Jones, 2010).



**Figure 2** – A) Species richness of bats in Africa based on potential distributions derived from niche modelling (see Appendix S1 for methods), showing a decline from east to west in southern Africa. Note also the low species richness in other arid zones of the continent, in particular the Sahara Desert in the north. The insert zooms in on the species richness in the southern African arid region, and highlights the spatial variability of this region. Note the relatively low richness in the flat and featureless Kalahari basin (in the centre of the map), compared with a higher richness in the drier, but topographically more varied Namib Desert (to the west). B) The number of species of bats currently known to occur in each of the four arid zones comprising the southern Africa arid region. See Tab. 1 for further details.

**Functional traits and habitat selection in arid regions**

The roosting sites and typical foraging habitats of bats in the arid region of southern Africa are presented in Tab. 2. The majority of these species roost in caves or other analogous conditions (such as mine adits), with only the vagrant *Eidolon helvum* roosting in trees. This is not surprising in an arid environment where, at least over the summer months, daytime temperatures may be very hot and trees offering shade are scarce (Rutherford and Westfall, 1986). Data for bat species from the other three arid regions located elsewhere in the world are presented in Supplemental Table S2. A common feature shared by species across these deserts is body mass: with the exception of the Australian *Macroderma gigas*, having an average body mass of 123 g, mass of bats in arid regions is relatively small ( $13.7 \pm 10.3$  g). We suggest that this is because, generally, only insectivorous bats inhabit these arid environments, as the larger fruit bats are unable to find sufficient food resources.

Results of the PCA exploring functional groups across the arid regions of the world are shown in Fig. 3. The first principal component (x-axis) is closely associated with echolocation, showing a gradient in peak frequency from low to high values. The second principal component is associated with flight skills (combining wing loading and aspect ratio), with highly manoeuvrable and low-speed species represented by low values, and poorly manoeuvrable and high-speed species by high values. These two principal components account for 99.9% of the variation in the data. What emerges from Fig. 3 is that there is significant overlap in the niches occupied by bats in the four regions. However, close inspection reveals that the bats of the southern

African arid region and those inhabiting the Negev desert, in contrast with those in the American and Australian deserts, are highly adapted to foraging and roosting in cluttered environments (occupying the lower-right corner of the graph). These are predominantly high duty-cycle echolocating bats from the families Hipposideridae and Rhinolophidae, but also include low duty-cycle, “whispering” bats from the Nycteridae. Additionally, the partial overlap reflects the fact that several genera and a number of species, e.g. *Rhinolophus clivosus* and *Pipistrellus rueppellii*, are shared by these two arid regions.

On the other hand, the southern African arid region lacks species adapted to foraging in open areas, and specifically those with low frequency calls and high flight speed (upper-left corner). This suggests that this particular foraging niche is not filled (or only partially filled) and/or is not available in this arid region. This pattern is unexpected for two major reasons. Firstly, this region comprises four biomes, as previously described, and hence exhibits a high degree of landscape heterogeneity leading to the expectation that it would offer the necessary resources to support a variety of bat functional groups. Secondly, open air foraging bats are mostly of the families Molossidae and Emballonuridae, both of which are common in other biomes of southern Africa as well as in other arid areas of the African tropical belt (e.g. Turkana desert, Webala et al., 2009). However, the Emballonuridae are not present in this arid region, and the Molossidae are represented by only two species. This reduced species richness might be an artefact of poor sampling techniques since open air foragers are not easily trapped in mist-nets except at roosting and drinking sites. Alternatively, this pattern might be driven by factors operating at a



**Table 2** – Roosting sites, foraging habitat, mean mass (g), wingloading (N/m<sup>2</sup>), aspect ratio and peak frequency of echolocation call (kHz) of arid region bats of southern Africa (Schoeman and Jacobs, 2008; Monadjem et al., 2010). These species are all insectivores, except *Eidolon* which is a frugivore.

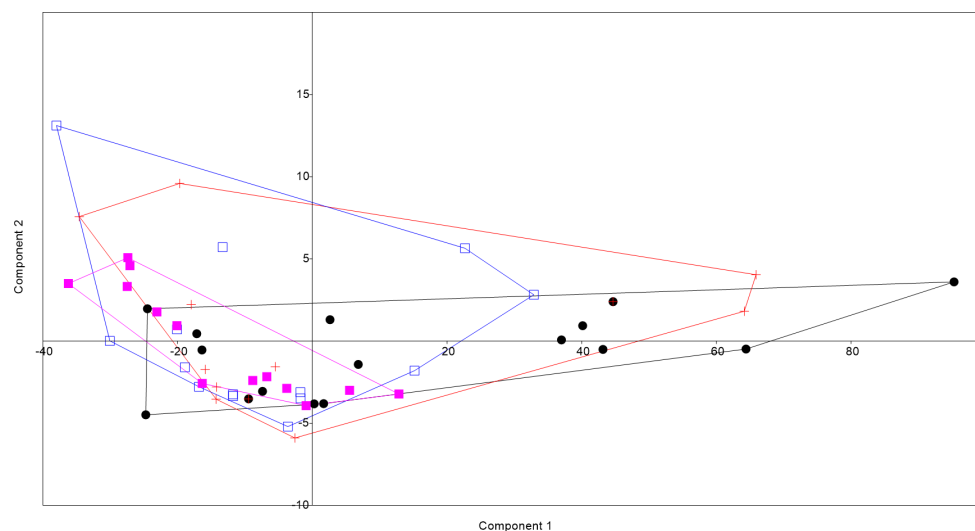
Species	Roost site	Foraging guild	Mass	Wing loading	Aspect ratio	Peak frequency
<i>Eidolon helvum</i>	Tree canopy		≈200	30.6	6.9	-
<i>Hipposideros caffer</i>	Cave, mine adit or sink hole	Clutter	8.5	6.6	6.3	142.3
<i>Rhinolophus capensis</i>	Cave, mine adit or sink hole	Clutter	10.8	7.2	6.0	83.9
<i>Rhinolophus clivosus</i>	Cave, mine adit or sink hole	Clutter	19.0	9.1	5.5	91.7
<i>Rhinolophus damarensis</i>	Cave, mine adit or sink hole	Clutter	8.8	7.8	6.3	87.1
<i>Rhinolophus denti</i>	Cave, mine adit or sink hole	Clutter	5.9	4.7	6.0	111.2
<i>Rhinolophus fumigatus</i>	Cave, mine adit or sink hole	Clutter	12.3	7.7	6.7	53.7
<i>Nycteris thebaica</i>	Cave, mine adit or sink hole	Clutter	12.6	6.3	5.3	90.0
<i>Sauromys petrophilus</i>	Rock crevice	Open	9.8	11.2	7.2	23.9
<i>Tadarida aegyptiaca</i>	Rock crevice, roof of houses	Open	16.0	13.1	8.1	22.7
<i>Miniopterus natalensis</i>	Cave, mine adit or sink hole	Open	11.6	10.7	7.0	49.7
<i>Cistugo seabrae</i>	Not known	Edge	3.8	5.7	6.9	47.0
<i>Eptesicus hottentotus</i>	Caves and rock crevices	Edge	18.1	10.3	6.3	30.6
<i>Laephotis namibensis</i>	Rock crevices	Edge	11.0	7.0	5.7	22.0
<i>Neoromicia capensis</i>	Under bark of trees, roof of houses	Edge	7.3	7.1	6.4	39.4
<i>Neoromicia zuluensis</i>	Crevice	Edge	5.8	5.7	6.4	48.4
<i>Pipistrellus rueppellii</i>	Crevice	Edge	6.8	6.8	6.3	37.3

broad regional scale. We suggest that this might be the extreme low winter night-time temperatures experienced in this arid zone, and that may be negatively impacting the abundance of insects flying high above the ground, restricting the occupation of this open air niche. However, this hypothesis is only tentative and the phenomenon deserves further investigation. This corroborates the findings of Tello and Stevens (2010), who identify seasonality as one of the main determinants of regional bat species richness on the American continent.

### Conclusion and Future Prospects

The bat fauna of the southern African arid region is poorly known. The few studies conducted are almost exclusively baseline surveys (often part of general mammal surveys) and, with few exceptions (e.g. Schoeman and Jacobs, 2008, 2011), do not address ecological or evolutionary questions. Hence, the ecology of the bat assemblages inhabiting the southern African arid region need further detailed investigation. Here we present two major reflections, originating from the patterns of bat species richness emerging from our analysis, that could be the subject of future ecological studies: a) at a regional scale and considering only bats from arid areas, landscape features might be more relevant than aridity gradients in determining bat diversity; and b) the functional group of the open air foragers is restricted in the southern African arid region, which is likely due to an unknown factor operating at a regional level.

Additionally, currently nothing is known about what ecosystem services are provided by bats in arid environments. In southern African savannahs to the east of the arid zone, bats may play an important ecological role by consuming pest insects in agro-ecosystems (Bohmann et al., 2011; Noer et al., 2012; Taylor et al., 2013). Fruit bats also play important roles in pollination and seed dispersal in African forests (Duncan and Chapman, 1999; Djossa et al., 2008). One profitable area of research relating to arid zone bats in agro-ecosystems would be investigating their role along the Gariiep River. This large river passes through the centre of the southern African arid region, delivering water to farmers along its banks. A wide variety of crops are grown here, including grapes in an otherwise hostile environment, at least from an agricultural perspective. Additionally, bats have been shown to be good indicators of a range of environmental changes (Jones et al., 2009; Rocha et al., 2017). However, their role as indicators of habitat quality in arid environments, though prospective, is completely unexplored. We advocate that research target this topic, and in particular we suggest that their potential as indicators of habitat degradation and recovery to be examined. If such a relationship was to be assessed, habitat quality, predicted to decrease with ongoing desertification of arid areas, could be monitored via surveying bats using acoustic tools, which allow for the collection of a large amount of data at relatively low costs. 🦇



**Figure 3** – Principal Components Analysis (PCA) including wing loading, aspect ratio and peak frequency of bats in four arid regions across the world: black dots (southern Africa), red crosses (Negev Desert, Israel), blue squares (western North America), purple squares (Australia).

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## Supplemental information

Additional Supplemental Information may be found in the online version of this article:

**Appendix S1** Distribution of bat species richness in sub-Saharan Africa.**Table S2** Functional traits of bats from the Israeli, North American and Australian arid regions.