

Sina M. Weier*, Valerie M.G. Linden, Ian Gaigher, Patrick J.C. White and Peter J. Taylor

Changes of bat species composition over altitudinal gradients on northern and southern aspects of the Soutpansberg mountain range, South Africa

DOI 10.1515/mammalia-2015-0055

Received March 24, 2015; accepted December 16, 2015

Abstract: In order to gain insight into the pattern of bat species composition over altitude and the environmental variables driving the observed pattern, we compared data from moist southern and drier northern aspects of the Soutpansberg range in northern South Africa. Acoustical monitoring and additional capturing of bats was used for analysis of species distribution patterns and comparisons of community composition. Bat activity generally followed a linear decline with increasing altitude, possibly related to reproductive females preferring lower altitudes. Species richness followed a hump-shaped distribution on the northern aspect and across the transect, whereas a

pattern of a linear decline was observed on the southern aspect. Our study strongly supports a previously published climate model for insectivorous bats which assumes that water availability linked with temperature determines the shape of altitudinal distribution in bat species. Step-wise selection from multiple regression models retained habitat type and/or measures of habitat structure in all final models, supporting several other studies in that vegetation correlated to altitude is a primary determinant of bat species distribution over altitude. This study also supports that the Soutpansberg is a biodiversity hotspot for bats and emphasises that conservation efforts should by no means ignore the lower altitudes.

Keywords: activity; Chiroptera; elevation; habitat; species richness.

*Corresponding author: Sina M. Weier, School of Life, Sport and Social Sciences, Edinburgh Napier University, Edinburgh, Scotland, UK; SARChI Chair on Biodiversity Value and Change, School of Mathematical and Natural Science, University of Venda, Thohoyandou, Limpopo, South Africa; Department of Zoology, School of Mathematical and Natural Sciences, University of Venda, Thohoyandou, Limpopo, South Africa; and Goro Game Reserve, PO Box 144, 0924 Vivo, South Africa, e-mail: sinamonika@gmail.com

Valerie M.G. Linden: SARChI Chair on Biodiversity Value & Change, School of Mathematical and Natural Science, University of Venda, Thohoyandou, Limpopo, South Africa; Department of Zoology, School of Mathematical and Natural Sciences, University of Venda, Thohoyandou, Limpopo, South Africa; and Resource Ecology Group, Wageningen University, Wageningen, The Netherlands

Ian Gaigher: SARChI Chair on Biodiversity Value & Change, School of Mathematical and Natural Science, University of Venda, Thohoyandou, Limpopo, South Africa; and Department of Zoology, School of Mathematical and Natural Sciences, University of Venda, Thohoyandou, Limpopo, South Africa

Patrick J.C. White: School of Life, Sport and Social Sciences, Edinburgh Napier University, Edinburgh, Scotland, UK

Peter J. Taylor: SARChI Chair on Biodiversity Value & Change, School of Mathematical and Natural Science, University of Venda, Thohoyandou, Limpopo, South Africa; and Core Team Member of Centre for Invasion Biology, School of Mathematical and Natural Science, University of Venda, Thohoyandou, Limpopo, South Africa

Introduction

While bats provide a wide range of valuable ecosystem services (Fenton 1997, Ducummon 2000, Kalka et al. 2008, Kunz et al. 2011), about one-quarter of all bat species are threatened with extinction (Mickleburgh et al. 2002). This proportion could rise quickly under progressing global climate change (Thomas et al. 2004). As suggested by Jones et al. (2009), bats are ideal indicator species to measure changes in the conditions of an ecosystem caused by anthropogenic pressure. Knowledge of altitudinal patterns of bat species richness will also enable conservationists to assess some of the possible outcomes of future climate change (Thomas et al. 2004) and other anthropogenic pressures (Jones et al. 2009).

A consensus exists that altitudinal gradients do not mirror latitudinal ones but that diversity usually peaks at intermediate altitudes (Rahbek 1995, Sanders and Rahbek 2012). Multiple factors underlie patterns of altitudinal distribution (Sanders and Rahbek 2012). Whereas the species-area effect and the mid-domain effect were long suggested to be the primary underlying causes of those

patterns, McCain (2007a) showed that area and space, both alone and together, were not sufficient in explaining altitudinal patterns of diversity. McCain (2007b) suggested that mid-altitudinal peaks in bat species richness are more likely to be found in temperate regions and a decline in species richness with altitude is most common in tropical regions. Unlike species richness, bat activity generally seems to decrease with altitude. This decrease of bat activity with altitude is suggested to be caused by a decline of reproductive females found with altitude related to lower temperatures and food availability (Grindal et al. 1999, Cryan et al. 2000, Russo 2002, Erickson and Adams 2003, Kanuch and Kristin 2006, Dunn and Waters 2012).

Very little research on altitudinal gradients in bat species richness or diversity focused on Africa so far (Curran et al. 2012). To our knowledge, the study of Linden et al. (2014) was the first attempt to analyse changes of bat species composition over an altitudinal gradient in South Africa. At Mount Mulanje in Malawi, Curran et al. (2012) found an altitudinal pattern of a “low plateau”, suggesting a decline of bat species richness starting at intermediate altitudes, with highest species richness at 1220 m. This pattern was significantly correlated with measures of habitat structure and also supported the global climate model of McCain (2007b). In the Soutpansberg Mountains in South Africa, Linden et al. (2014) found a decline in species richness and diversity with altitude, as suggested for tropical regions by McCain (2007b). The study also found vegetation type, correlated with altitude, to be the main underlying factor explaining the observed pattern. However, this study was limited to the southern aspect of the Soutpansberg. Although temperature is not expected to vary greatly between the northern and the southern aspect, the southern aspect has a higher annual precipitation (up to 3233 mm in the eastern Soutpansberg and about 720 mm in the west associated with this study), whereas the precipitation on the northern aspect is much lower (367 mm of mean annual rainfall at Waterpoort near the study site) because of a rain-shadow effect (Mostert et al. 2008).

By analysing a complete altitudinal transect of the Soutpansberg, the objective of this research was to gain insight into the pattern of altitudinal distribution of bat species, the underlying factors driving the observed pattern and the implications of this pattern for conservation. For this purpose, we extended the study area of Linden et al. (2014) to the northern aspect of the mountain range, in order to compare the data from both studies. We also tested the results against the climate model of McCain (2007b). Based on the assumption of McCain (2007b) that water availability is a main factor in determining

the shape of altitudinal distribution in bats, we hypothesise that, in contrast with the more tropical southern aspect which shows a decline with altitude, on the drier northern aspect, the altitudinal pattern of bat species richness should follow a humped shaped pattern with a mid-altitudinal peak in bat species richness. Based on the studies of Linden et al. (2014) and Curran et al. (2012), we further expect vegetation type and measures of habitat structure, correlated to climate, to be the main variables explaining the distribution of bat species over altitude. We also tested the “mid-domain effect” which specifies that most ranges of species overlap towards intermediate altitudes (the “mid-domain”) (Colwell and Lees 2000, McCain 2005, Kryštufek et al. 2011).

Materials and methods

Study area

The study area is located in the western Soutpansberg of the northern South African province, Limpopo (Figure 1). Whereas, a previous study (Linden et al. 2014) was conducted in the Luvhondo Private Nature Reserve (LPNR) on the southern aspect of the Soutpansberg, the present study extended the study area to the northern aspect, exactly opposite to the LPNR. As described by Mucina and Rutherford (2006), the habitat types found within the study area are Soutpansberg Mountain Bushveld (SMB), Northern Mistbelt Forest (NMF), Soutpansberg Summit Sourveld (SSS), Makhado Sweet Bushveld (MSB) and Musina Mopane Bushveld (MMB) (Figure 1).

The Soutpansberg is nationally recognised as a centre of endemism and biodiversity (Mostert et al. 2008). It also forms part of the North-Eastern Escarpment Bioregion which has been highlighted as one of the nine priority areas for conservation by the South African National Biodiversity Institute (SANBI) and falls within the buffer zone of the UNESCO Vhembe Biosphere Reserve (UNESCO 2010). The Soutpansberg forms a South African species richness hotspot for bats (Taylor et al. 2013).

Data collection

For the purpose of this study, we collected data along an altitudinal transect of 769–1624 m a.s.l. on the northern aspect of the Soutpansberg, South Africa. Data collection took place from the end of February to May 2014 with a total of 22 nights of recordings. Data collection for the

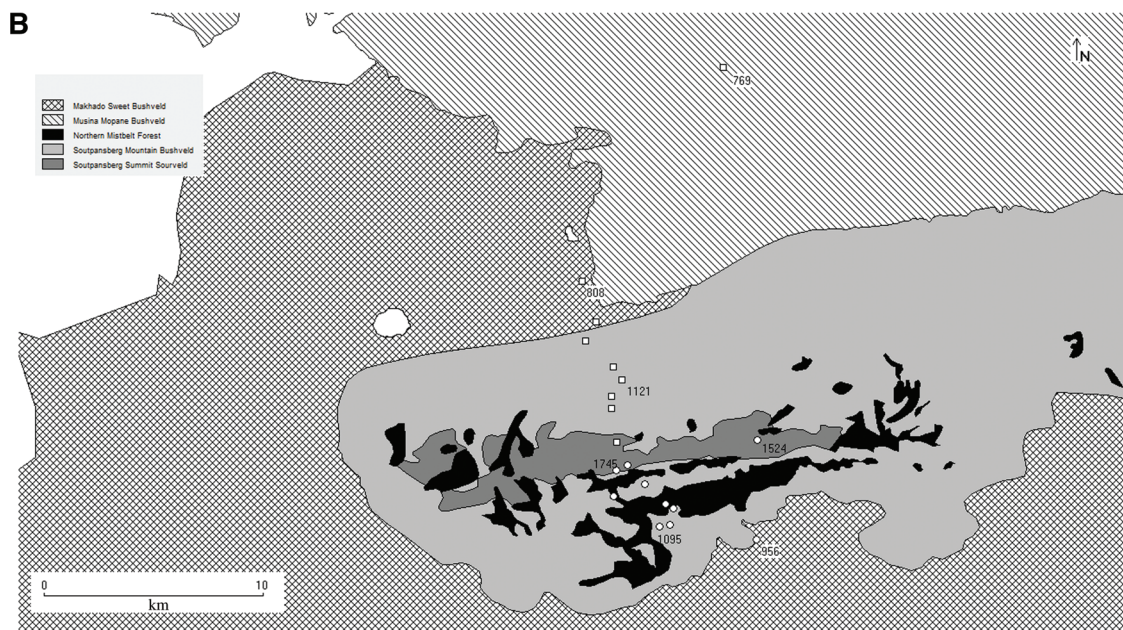
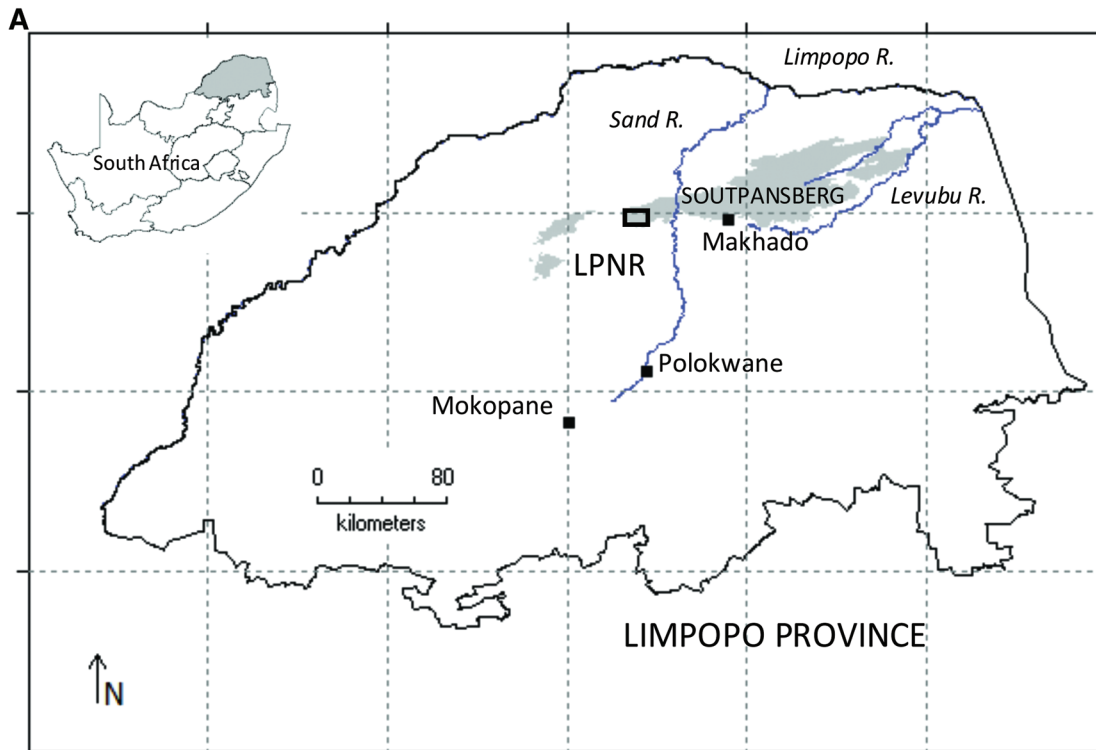


Figure 1: Map showing (A) the location of the study area in the Limpopo Province of South Africa and (B) the habitat types within the western Soutpansberg, South Africa, indicating bat sampling sites on the southern (circles) and northern (squares) aspects (Robert J. Hijmans, Version 7.5.0.0).

study of Linden et al. (2014) took place along a transect of 956–1747 m a.s.l. on the southern aspect of the western Soutpansberg from October to December 2011, with a total of 18 nights of recordings. The altitudinal range of our study site, therefore, extends to the top of Mount Letjume

which is the highest peak of the Soutpansberg mountain range.

Additionally to acoustical monitoring, we captured bats with an Austbat Harp trap (Faunatech Austbat, Bairnsdale, Victoria, Australia) and several mist nets (Ecotone,

Gdynia, Pomerania, Poland) at each sampling site. Release calls of captured bats were taken for comparison with the nightly recordings. The captured bats were identified by using the identification key of Monadjem et al. (2010). Positively identified species were released after measurements, release calls and photographs were taken. Unknown or difficult-to-identify species were collected as voucher specimens (Permit No. 001-CPM403-00010 from the Limpopo Department of Economic Development, Environment and Tourism) provisionally identified at the University of Venda by PJT and deposited in the mammal collection of the Durban Natural Science Museum.

We caught and acoustically monitored bats for two nights at each sampling site by using either the SM2BAT (Wildlife Acoustics, Inc., Maynard, MA, USA), the Anabat SD1 or SD2 (Titley Scientific, Columbia, MO, USA) for passive monitoring. The bat detector was placed in an elevated position, usually a tree, pointing in the direction of expected flyways. To account for differences in foraging behaviours of bats linked to vegetation densities (Kusch et al. 2004, Monadjem et al. 2010) we placed the bat detector in an open habitat for one night of recordings and, wherever possible, in an area with closed vegetation for the other night. The open vegetation of Soutpansberg Summit Sourveld, for example, offers no possibilities to sample in closed habitat. The bat detector, the trap and nets were set up 1 h before sunset to ensure that the expected peak of bat activity right after sunset was sampled (Kunz and Kurta 1988, Barlow 1999). The nets were left up for 3 h in which they were continuously monitored, while the bat detector and the harp trap remained set on site until after sunrise. Whereas the harp trap was set in forest gaps, the mist nets were set in the more open habitats.

Apart from altitude which was measured by means of a Garmin Etrex GPS [Garmin (Europe) Ltd, Southampton, Hampshire, UK], the control variable cloud cover was measured 1 h before sunset and the illumination of the moon was recorded for each night (Time and Date AS 2014). The daily mean temperature and rainfall were recorded by accessing data of one of the four available weather stations on the northern aspect (807, 1221, 1400 and 1747 m). Furthermore, we recorded the presence or absence of water (within 50 m of the harp trap). The vegetation structure was measured subjectively above the bat detector by both observers estimating the canopy cover on a scale from 0% to 100% in 10% steps and the vegetation density (1=*uncluttered and background clutter*, 2=*intermediate clutter*, 3=*dense clutter*) 20 m² around the bat detector, adjusting the method of Curran et al. (2012). Additionally, the overall clutter type (open or closed) was recorded as in the previous study (Linden et al. 2014).

Data analysis

AnalookW (version 0.3.8.13; Corben 2006) was used to analyse the recorded calls by comparing them against release calls and by referring to Monadjem et al. (2010) and Taylor et al. (2013) for call identification. Because of an overlap in call parameters, following Taylor et al. (2013), we combined several species into groups for calculation of final indices (Supplemental Appendix 1).

EstimateS (version 9.1.0, Colwell 2013) was used to calculate the bat activity (individuals computed) and the estimated species richness (Chao2) for each sampling site per night, and to plot rarefaction curves, whereby 1 h of passive recordings equalled one sample. For statistical analyses, the program R (version 3.1.0; R Core Team 2014) was used.

To test whether the mid-domain effect (MDE) is a significant predictor of the total number of species observed (observed species richness) over altitude, the programme RangeModel (version 5.0, Colwell 2011) was used. The species richness patterns on each aspect were compared to null model predictions with a Monte Carlo simulation (50,000 resamples) using empirical range sizes within a “discrete domain” (Colwell and Lees 2000, Dunn et al. 2006). The model domain of each aspect was bound by the altitudinal range of each study area (McCain 2005). We applied simple linear regression to test the correlation between empirical and predicted values (Taylor et al. 2015).

Effect of altitude and aspect

Due to the possibility of curvature (Crawley 2007), we used both linear and non-linear (polynomial) regression models to test the response of activity and species richness to both altitude (continuous) and aspect (categorical). After testing all models for normal distribution of the response variables (Shapiro-Wilk test) and constant errors variance (Breusch-Pagan test), generalised linear models (GzLM) were applied. As we found non-normality in both response variables, their logarithms were used. As several of the GzLM using the Poisson distribution were overdispersed, we applied GzLM with a negative binomial distribution to all models. This also allowed for consistency in modelling with the Akaike Information Criterion (AIC) used for later analyses (Ver Hoef and Boveng 2007). Model fit was tested using a likelihood ratio test for negative binomial models. The final model for each index was then selected by means of a step-wise regression based on the Akaike information criterion (AIC).

Environmental variables

We further tested which environmental variables are significant predictors of bat activity and estimated species richness looking at the northern aspect and the complete transect. Continuous environmental predictors included altitude, canopy cover, cloud cover, rainfall, temperature and vegetation density, while categorical variables included presence or absence of water, open or closed clutter as well as the factor of the habitat type (Figure 1). Since altitude was collinear with habitat in all models (Figure 2) it was excluded from all models. We used a general linear model (GLM) to model species richness as error variance was constant and error distribution was normal; this was not the case for bat activity, so we used a negative binomial GzLM to model this variable.

We used step-wise multiple regressions based on AIC values to analyse which variables have a significant influence on bat activity and estimated richness (Crawley 2007, Sanders et al. 2007). The same modelling was repeated with the data from both aspects, excluding the continuous variables which were available solely from the study on the northern aspect (canopy cover, rainfall, temperature, vegetation density) but including the variable moon phase. Because the response variables of bat activity and estimated richness showed non-normal distribution they were both modelled in GzLM with negative binomial distribution. As before, we selected final models by means of an AIC-based step-wise multiple regression.

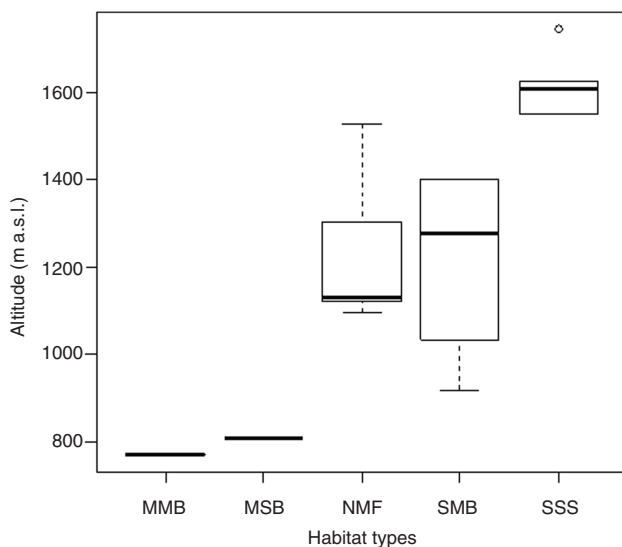


Figure 2: Distribution of habitat types over altitude in the western Soutpansberg, South Africa [Soutpansberg Mountain Bushveld (SMB), Northern Mistbelt Forest (NMF), Soutpansberg Summit Sourveld (SSS), Makhado Sweet Bushveld (MSB) and Musina Mopane Bushveld (MMB)].

Complementarity and community composition

The β diversity for the northern and the southern aspect was calculated, using the abundance-based and bias-corrected Chao-Jaccard index (Colwell 2013). Summary tables were used to compare for similarities and differences in species found on the northern and southern aspect and their “functional foraging groups” according to Monadjem et al. (2010).

Results

From a total of 3741 calls recorded during this study, we positively identified 3524 calls into 16 different species or species groups. In addition, we caught a total of eight species. Out of these eight species, two species, the slit-faced bat *Nycteris thebaica* (Saint-Hilaire, 1813) and the fruit bat *Epomophorus wahlbergi* (Sundevall, 1846), were not recorded on the bat detector. Thus, we found a total of 18 species or species groups, belonging to eight different families on the northern aspect (Supplemental Appendices 1 and 2).

Mid-domain effect model predictions

The predictions of the MDE null models failed to predict the observed richness pattern for both aspects (Figure 3).

MDE model south ($F_{(1,7)}=1.34$; $p=0.28$, adjusted $r^2=0.04$).

MDE model north ($F_{(1,7)}=0.001$; $p=0.96$, adjusted $r^2=-0.14$).

Effect of altitude and aspect

Comparison between simple linear and polynomial regression models showed evidence for curvature in one of the four models. The model for the estimated richness on the northern aspect of the mountain range was a significantly better fit for polynomial data ($\chi^2=6.93$, $df=1$, 19 , $p=0.008$). Bat activity declined with increasing altitude on both the southern and northern aspect (Figure 4). The estimated richness index showed the same negative linear relationship for the southern aspect. However, we found a hump-shaped pattern with a slight increase up to about 1000 m and a subsequent decline for the estimated richness on the northern aspect (Figure 5).

When modelling included the data from both aspects, the model for estimated richness was, again, a

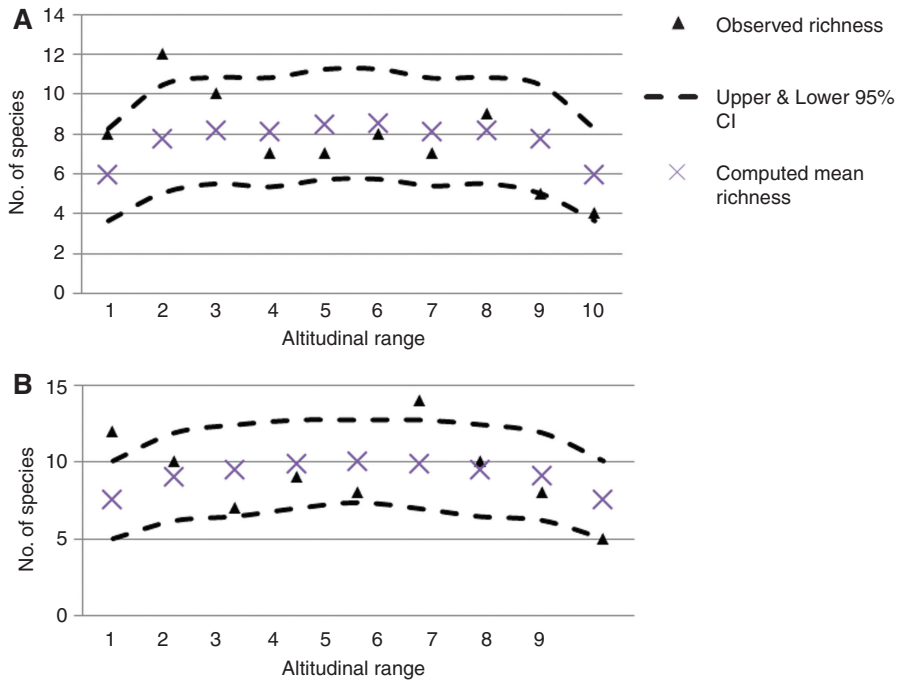


Figure 3: Observed species richness plotted against the altitudinal range of bat species in the western Soutpansberg, South Africa, with curves of the 95% confidence intervals and mean richness predictions computed with RangeModel for the southern (A) and northern (B) aspects.

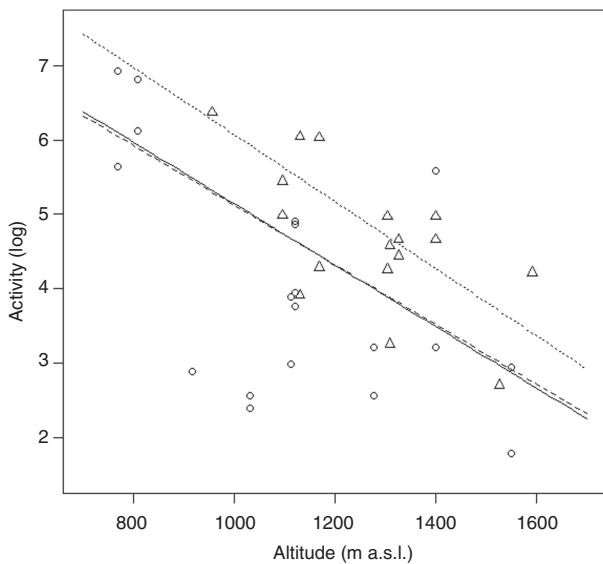


Figure 4: Bat activity predicted from regression models for the complete transect (line), the southern (dotted) and northern (dashed) aspects of the western Soutpansberg, South Africa. Raw data points are shown for the southern (triangle) and northern (circles) aspects.

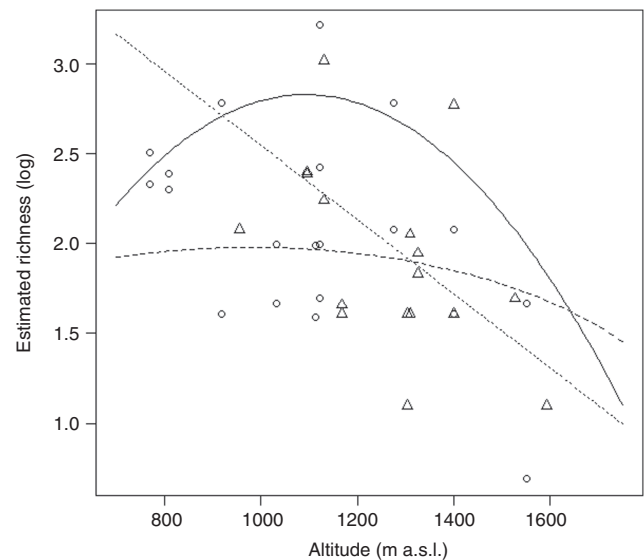


Figure 5: Estimated richness of bats predicted from regression models for the complete transect (straight line), the southern (dotted) and northern (dashed) aspects of the western Soutpansberg, South Africa. Raw data points are shown for the southern (triangle) and northern (circles) aspects.

significantly better fit for polynomial data ($\chi^2=10.13$, $df=1$, 34 , $p=0.001$). The step-wise selection performed on the GzLM of bat activity retained the two variables altitude ($\chi^2=25.15$, $df=1$, 37 , $p<0.001$) and aspect ($\chi^2=4.83$, $df=1$, 36 ,

$p=0.027$) in the final model. Bat activity was higher on the southern aspect. For the GzLM of estimated richness, the final model retained the variable altitude ($\chi^2=17.93$, $df=1$, 37 , $p<0.001$) and its quadratic term. While bat activity

showed a steady decrease with altitude, estimated richness showed a hump-shaped pattern.

Environmental variables

Northern aspect

For the GzLM on bat activity, step-wise selection of the final model retained three of the nine variables (clutter type, habitat type and water). Of these three variables, only water ($\chi^2=4.13$, $df=1$, 16 , $p=0.041$) and habitat type ($\chi^2=62.48$, $df=4$, 17 , $p<0.001$) had significant coefficients (Table 1). The presence of water negatively affected bat activity and higher activity was found in Musina Mopane Bushveld and Makhado Sweet Bushveld (low altitude habitat types) than in Soutpansberg Summit Sourveld.

In the step-wise selection of the GLM on estimated richness, the final model retained two (clutter and habitat type) out of nine variables ($F_{(5,16)}=3.36$, $p=0.028$, adjusted

$r^2=0.36$). From these variables, only the coefficients of habitat type were significant ($F_{(4,16)}=4.11$, $p=0.017$). Estimated richness was highest in Musina Mopane Bushveld and decreased in Makhado Sweet Bushveld, Northern Mistbelt Forest and Soutpansberg Mountain Bushveld. Lowest values of estimated richness were recorded in Soutpansberg Summit Sourveld.

Complete transect

For the GzLM on bat activity, step-wise selection of the final model retained four of the six variables (clutter type, moon, habitat type and aspect). Of these four variables selected for the final model, only clutter type ($\chi^2=4.05$, $df=1$, 37 , $p=0.044$), habitat type ($\chi^2=36.37$, $df=4$, 33 , $p<0.001$) and aspect ($\chi^2=17.26$, $df=1$, 32 , $p<0.001$) had significant coefficients (Table 2). We found that bat activity was higher where the clutter type was “open” and on the southern aspect of the study area. Highest bat activity was recorded in the “lowland” habitat types of Musina Mopane Bushveld and Makhado Sweet Bushveld, while lowest bat activity was recorded in the high-altitude habitat of the Soutpansberg Summit Sourveld (Figure 6).

Table 1: Final models (bold) testing the environmental variables on the northern aspect of the western Soutpansberg, South Africa, describing the variation bat activity and estimated species richness.

	df	Test statistic	p-Value	Estimate	SE
Estimated richness					
Canopy cover ^a	1, 10	0.246	0.810		
Vegetation density ^a	1, 10	0.131	0.898		
Clutter type open	1, 16	2.493	0.024	8.371	3.358
Habitat type (MSB)	4, 16	0.688	0.501	3.335	4.847
Habitat type (NMF)	4, 16	1.034	0.316	4.482	4.335
Habitat type (SMB)	4, 16	-0.677	0.508	-2.434	3.595
Habitat type (SSS)	4, 16	-2.409	0.028	-9.485	3.938
Cloud cover ^a	1, 10	-0.264	0.797		
Rainfall ^a	1, 10	-0.758	0.466		
Temperature ^a	1, 10	-0.786	0.449		
Presence of water ^a	1, 10	-0.906	0.386		
AIC					136.06
Activity					
Canopy cover ^a	1, 14	-0.861	0.388		
Vegetation density ^a	1, 12	1.224	0.220		
Clutter type open	1, 15	1.704	0.088	1.039	0.610
Habitat type (MSB)	4, 17	0.597	0.550	0.523	0.875
Habitat type (NMF)	4, 17	-2.142	0.032	-1.679	0.784
Habitat type (SMB)	4, 17	-4.723	<0.001	-3.993	0.845
Habitat type (SSS)	4, 17	-6.159	<0.001	-6.274	1.018
Cloud cover ^a	1, 20	-1.034	0.301		
Rainfall ^a	1, 11	-0.990	0.322		
Temperature ^a	1, 10	-0.789	0.430		
Presence of water	1, 16	-2.320	0.020	-1.628	0.701
AIC					234.67

^aParameter estimates retrieved from initial global models.

Table 2: Final models (bold) testing the environmental variables of the complete transect of the western Soutpansberg, South Africa, describing the variation bat activity and estimated species richness.

	df	Test statistic	p-Value	Estimate	SE
Estimated richness					
Clutter type open ^a	1, 35	1.054	0.291		
Habitat type (MSB)	4, 34	-0.161	0.872	-0.078	0.485
Habitat type (NMF)	4, 34	-0.610	0.542	-0.221	0.363
Habitat type (SMB)	4, 34	-0.718	0.472	-0.264	0.368
Habitat type (SSS)	4, 34	-3.872	<0.001	-1.885	0.486
Cloud cover ^a	1, 37	0.690	0.490		
Moon ^a	1, 36	0.010	0.992		
Presence of water ^a	1, 30	-0.265	0.790		
Aspect South ^a	1, 29	-0.416	0.677		
AIC					223.0
Activity					
Clutter type open	1, 36	1.455	0.145	0.525	0.360
Habitat type (MSB)	4, 32	-0.364	0.721	-0.357	1.022
Habitat type (NMF)	4, 32	-3.351	<0.001	-2.696	0.804
Habitat type (SMB)	4, 32	-4.075	<0.001	-2.997	0.735
Habitat type (SSS)	4, 32	-5.511	<0.001	-4.572	0.829
Cloud cover ^a	1, 37	-0.078	0.938		
Moon	1, 37	-1.624	0.104	-0.008	0.004
Presence of water ^a	1, 30	-0.758	0.448		
Aspect South	1, 31	3.987	<0.001	1.337	0.335
AIC					441.66

^aParameter estimates retrieved from initial global models.

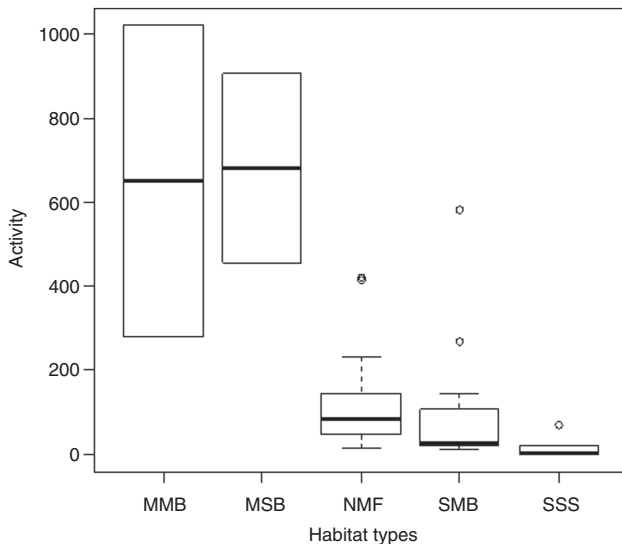


Figure 6: Bat activity within the different habitat types of the western Soutpansberg, South Africa (for abbreviations, see Figure 2).

Only habitat type was retained in the final model of estimated species richness ($\chi^2=27.54$, $df=4$, 35 , $p<0.001$). Highest values of estimated richness were found in Musina Mopane Bushveld and lowest values in Soutpansberg Summit Sourveld (Figure 7).

Habitat type is the only variable retained in all final models. As found in the previous study (Linden et al. 2014), altitude had a significant effect on the habitat type found ($F_{(4,35)}=20.29$; $p<0.001$, adjusted $r^2=0.66$). Figure 2 shows that Soutpansberg Summit Sourveld is reflective of high altitudes as Makhado Sweet Bushveld and Musina Mopane Bushveld are reflective of low altitudes.

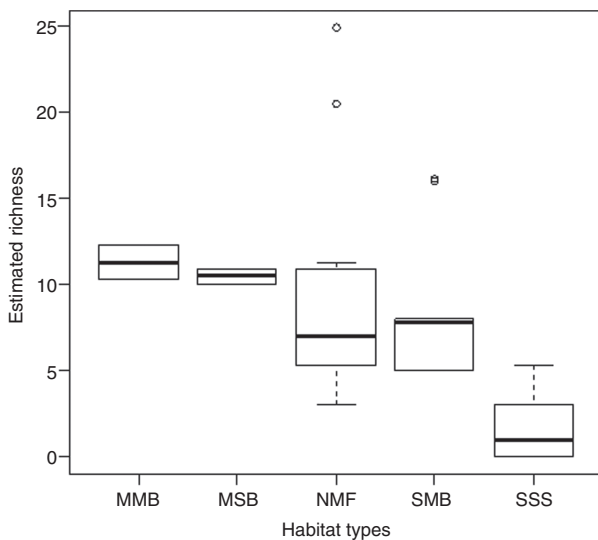


Figure 7: Estimated bat species richness within the different habitat types of the western Soutpansberg, South Africa.

Complementarity and community composition

Several of the species encountered differed between the study sites, on the northern and southern aspect of the Soutpansberg mountain range.

The species *Myotis welwitschii* (Gray, 1866), *Mops midas* (Sundevall, 1843) and *Rhinolophus cf. blasii* (Peters, 1867) were found only on the southern aspect, whereas the species *Hipposideros caffer* (Sundevall, 1846), *Nycteris thebaica*, *Neoromicia nana* (Peters, 1852), *Scotophilus viridis* (Peters, 1852) and *Taphozous mauritanus* (Saint-Hilaire, 1818) were found only on the northern aspect. The abundance-based and bias-corrected Chao-Jaccard index for comparing the β diversity between the northern and the southern aspect of the Soutpansberg was 0.865.

Looking at the distribution of species or species groups over altitude on the northern aspect, the only species present up to an altitude of 1550 m were *Chaerephon ansorgei* (Thomas, 1913), *Neoromicia capensis* (Smith, 1829), *Taphozous mauritanus* and the species groups 1 [*Chaerephon pumilus* (Cretzschmar, 1826), *Mops condylurus* (Smith, 1833) and *Tadarida aegyptiaca* (Saint-Hilaire, 1818)] and 3 [*Miniopterus natalensis* (Smith, 1833) and *Pipistrellus rusticus* (Tomes, 1861)]. Species group 2 [*Neoromicia zuluensis* Roberts, 1924 and *Pipistrellus hesperidus* (Temminck, 1840)], *Rhinolophus simulator* (Andersen, 1940), *Scotophilus dinganii* (Smith, 1833) and *Scotophilus viridis* were found up to 1400 m, while *Eptesicus hottentotus* (Smith, 1833) was found up to 1121 m and *Neoromicia nana* was not found at any sites higher than 1031 m. None of the horseshoe bats (*Rhinolophidae*) was found at sites higher than 1400 m. The fruit bat *Epomophorus wahlbergi* was not caught at sites above 808 m.

Discussion

The mid-domain effect

The mid-domain effect (MDE) did not explain the variation of observed species richness over altitude in this study. The hypothesis of the MDE is based on the assumption that the range of each species is directed towards one end of the domain (for altitudinal studies, the sea would be one end and the mountain summit the other) and, therefore, most ranges overlap in the “mid-domain”. On neither the northern nor the southern aspect were any bat species observed to be restricted to or towards the higher altitudes.

Effect of altitude and aspect

While, the pattern of bat activity was not affected by the climatic differences in aspect, our results support the assumption that water availability linked with temperature is the underlying factor in determining the shape of altitudinal distribution in bat species based on McCain (2007b). The altitudinal pattern of bat species richness differed between the drier northern and the more mesic southern aspect, in that the altitudinal pattern on the northern aspect was hump shaped with a mid-altitudinal peak, while the pattern on the southern aspect followed that of a linear decrease with increasing altitude. These results are consistent with McCain's (2007b) theory that highest richness on an altitudinal gradient is found where high water availability coincides with high temperatures. When comparing three mountains in Mexico, two of which show a dry climate and one with a wet climate, McCain (2007b) found a decrease in species richness at the wet mountain and a hump-shaped pattern at the mountains with dry climates.

Looking at the climate model of McCain (2007b, Figure 4C) in more detail, the suggested peak in bat species richness according to the “global analyses of insectivores” bats for the study area (23°S) would be at roughly 1000 m which is a good fit to the predicted richness on the northern aspect (Figure 5). Looking at the complete transect, the predicted values for estimated richness peak at about 1100 m (Figure 5), which is still a significant fit for the climate model according to the study of Curran et al. (2012). This strongly supports the predictive ability of McCain's (2007b) climate model even though the study did not include any data from the African continent.

The changeover from a linear decline in species richness observed on the southern aspect to the hump-shaped pattern found when looking at the whole transect also agrees with Rahbek's suggestion (Rahbek 2005) that on a local scale, the hump-shaped pattern of species richness increases with studies sampling a large extent or the complete altitudinal gradient.

The pattern of bat activity did not change between northern and southern aspects, although activity was generally higher on the southern aspect which could be related to the higher productivity of this aspect (Terborgh 1977). We suggest that the pattern of bat activity declining steadily with increasing altitudes could also be caused by reproductive females avoiding higher altitudes.

Environmental variables

Step-wise selection retained habitat type in all final models and a measure of habitat structure (clutter type)

in one. Several other studies on bat species distribution support this assumption (Curran et al. 2012). Similarly, Jaiberg and Guisan (2001) found altitude, as well as vegetation structure, to be predictive for the community composition and species distribution of bats in a temperate environment. Looking at a study of Old World fruit bat (Pteropodidae) distribution over altitude, Juste and Perez del Val (1995) found a decline of species richness with altitude, which is suggested to be influenced by variations in habitat. The study of Lopez-Gonzalez et al. (2012) found that the metacommunity composition in Mexican bats is correlated to both heterogeneity in vegetation along a humidity gradient and an altitudinal gradient. Additionally, temperature, vegetation and precipitation, suggestively correlated with altitude, proved best in predicting bat species distribution in the study of Wang et al. (2003).

Complementarity and community composition

As we expected because of the difference in conditions between aspects, not all species are shared between the northern and the southern aspect of the Soutpansberg and the β diversity index was, therefore, not close to 1 (0.865). The absence of the “open-air forager” *Mops midas* on the northern aspect is puzzling to us since it should provide plenty of ideal “open” habitat. Meanwhile, the absence of *Myotis welwitschii*, a known “paramontane” species, might be explained by a lack of suitable forest habitat in connection to lower altitudes as found on the southern aspect (Monadjem et al. 2010). Being a “clutter feeder”, the species *Rhinolophus cf. blasii* might also prefer the more forested southern aspect. A lack of suitable caves serving as roost sites might be another variable explaining why this species was not encountered on the northern aspect (Monadjem et al. 2010).

As in the previous study (Linden et al. 2014), our study did not identify any species as being “upland” species restricted to higher altitudes as found by Kanuch and Kristin (2006) and Delgado-Jaramillo et al. (2011). The study of Presley et al. (2012) found that the metacommunity structure along an altitudinal gradient differs between bats, rodents and birds. While altitude seems to influence how the metacommunities are structured, bat communities are overlapping whereas groups of birds replace each other along the gradient, even more so do rodents (Taylor et al. 2015). It is suggested that bird and rodent communities are structured according to the microhabitat they are specialized on, whereas bat community structure might be influenced more by the temperature, productivity and food, that particular species tolerate.

Possible bias

Sampling effort was very similar between the two studies and across the altitudinal transect; however, the study area on the northern aspect was spatially further extended, reaching into the lowland habitat types of Musina Mopane Bushveld and Makhado Sweet Bushveld. These were the only habitat types where baobab trees, a favoured roost site for many bats and important food source for fruit bats, could be found. The presence of baobab trees likely contributes to the high bat activity found in these two habitat types. While area is suggested to explain the pattern of latitudinal species distribution (Terborgh 1973, Rosenzweig 1992), the review of McCain (2007a) concluded that area and space, both alone and together, are not sufficient in explaining altitudinal patterns of mammal diversity. Although we did not account for the decrease in area with increasing altitude, Linden et al. (2014) showed that the habitat type with the greatest areal representation (Soutpansberg Mountain Bushveld) showed lower species richness than Northern Mistbelt forest having a much lower area; this is also true on the northern aspect (Figure 1).

The climate in the study area can be divided into two seasons: a warm, wet summer and a cold, dry winter (Mostert et al. 2008). Both the current and the previous study took place in the summer season; however, the southern aspect was sampled in the beginning of summer (October to December) while sampling on the northern aspect took place towards the end of summer (February to May). No significant seasonal bias is expected in this study since a previous study on the southern aspect suggested that seasonal bias of recorded bats is low (Sape 2011).

We used the abundance-based and bias-corrected species richness estimator “Chao2” to account for the likely underestimation of species when using the observed species richness (Supplemental Appendix 3a). However, based on several suspected species which could not be confirmed and the difficulty in recording some species, such as *Nycteris* (also called “whispering bats”), we suggest that further sampling of the study area will reveal additional and potentially interesting species (Supplemental Appendix 3b). Further, the fact that neither temperature nor water availability could be linked to altitudinal bat species distribution directly might be biased by the means of measuring these variables. Water availability should possibly include further measurements such as orographic mist received and temperature recordings might be enhanced by additional mean annual or monthly temperature recordings for each site.

Implications for conservation

Following Curran et al. (2012), this study supports the strong predictive ability of McCain’s (2007b) climate model and, therefore, its implementation as an assessment tool for mountainous areas where sufficient data are lacking and/or difficult to acquire. Furthermore, our results confirm the Soutpansberg area as a “bat biodiversity hotspot” and support its status as a “priority area for conservation”. Disassembling species groups, a total of 25 species of bats were found during this study (including the unidentified *Rhinolophus* species) which included species from all eight families of bats and is about 20% of all bat species found in Southern Africa. As only a relatively small transect of the Soutpansberg was sampled for this study within a total time period of about 3 months, we expect the true species richness to be even higher.

Acknowledgments: Dave and Karen Dewsnap from the Goro Game Reserve are thanked for not only providing access and accommodation but also lots of logistical aid. We are grateful to the Lajuma Research Centre team with Oldrich van Schalkwyk for their continued support and access to their weather data. The owners of the farm Sigurwana are thanked for providing access to their property. Many thanks are due to Stefan Foord and Caswell Munyai for access to their weather data. The University of Venda and the National Research Foundation (NRF) and Department of Science and Technology (DST), through the SARChI Research Chair on Biodiversity Value & Change in the Vhembe Biosphere Reserve is thanked for funding this project and providing the equipment.

References

- Barlow, K. 1999. Bats. Expedition and field techniques. Royal Geographical Society, London, UK. pp. 69.
- Colwell, R.K. 2011. Range model- tools for exploring and assessing geometric constraints on species richness (the mid-domain effect) along transects. Published at: <http://viceroy.eeb.uconn.edu/RangeModel/>.
- Colwell, R.K. 2013. EstimateS: statistical estimation of species richness and shared species from samples. Version 9 and earlier. Users guide and application. Published at: <http://purl.oclc.org/estimates>.
- Colwell, R.K. and D.C. Lees. 2000. The mid-domain effect: geometric constraints on the geography of species richness. *Trends Ecol. Evol.* 15: 70–76.
- Corben, C. 2006. AnalookW for bat call analysis using ZCA. Published at: www.hoarybat.com.

- Crawley, M.J. 2007. *The R book*. John Wiley & Sons Ltd, Chichester, UK. pp. 950.
- Cryan, P.M., M.A. Bogan and S.J. Altenbach. 2000. Effect of elevation on distribution of female bats in the Black Hills. *South Dakota. J. Mammal.* 81: 719–725.
- Curran, M., M. Kopp, J. Beck and J. Fahr. 2012. Species diversity of bats along an altitudinal gradient on Mount Mulanje, southern Malawi. *J. trop. Ecol.* 28: 243–253.
- Delgado-Jaramillo, M., M. Machado, F.J. García and J. Ochoa. 2011. Murciélagos (Chiroptera: Mammalia) del Parque Nacional Yurubí, Venezuela: listado taxonómico y estudio comunitario. *Rev. Biol. Trop.* 59: 1757–1776.
- Ducummon, S.L. 2000. Ecological and economic importance of bats. In: *Proceedings of bat conservation and mining: A technical interactive forum held November 14–16, 2000, at the Airport Hilton, St. Louis, Missouri*. U.S. Department of Interior, Office of Surface Mining, Alton, IL and Coal Research Center, Southern Illinois University, Carbondale, IL. pp. 12.
- Dunn, J.C. and Waters, D.A. 2012. Altitudinal effects on habitat selection in two sympatric pipistrelle species. *Mammalia* 76: 427–433.
- Dunn, R.R., R.K. Colwell and C. Nilsson. 2006. The river domain: why are there more species halfway up the river? *Ecography* 29: 251–259.
- Erickson, J.L. and M.J. Adams. 2003. A comparison of bat activity at low and high elevations in the Black Hills of Western Washington. *Northwest Sci.* 77: 126–130.
- Fenton, B.M. 1997. Science and the conservation of bats. *J. Mammal.* 78: 1–14.
- Grindal, S.D., J.L. Morissette and R.M. Brigham. 1999. Concentration of bat activity in riparian habitats over an elevational gradient. *Canadian J. Zool.* 77: 972–977.
- Jaiberg, C. and A. Guisan. 2001. Modelling the distribution of bats in relation to landscape structure in a temperate mountain environment. *J. appl. Ecol.* 38: 1169–1181.
- Jones, G., D.S. Jacobs, T.H. Kunz, M.R. Willig and P.A. Racey. 2009. *Carpe noctem: the importance of bats as bioindicators*. *Endang. Spec. Res.* 8: 93–115.
- Juste, J.B. and J. Perez del Val. 1995. Altitudinal variation in the subcanopy fruit bat guild in Bioko Island, Equatorial Guinea, Central Africa. *J. trop. Ecol.* 11: 141–146.
- Kalka, B.M., A.R. Smith and E.K.V. Kalko. 2008. Bats limit arthropods and herbivory in a tropical forest. *Science* 320: 71.
- Kanuch, P. and A. Kristin. 2006. Altitudinal distribution of bats in the Pol'ana Mts area (Central Slovakia). *Biologia* 61: 605–610.
- Kryštufek, B., N.R. Doneva and J. Skok. 2011. Species richness and distribution of non-volant small mammals along an elevational gradient on a Mediterranean Mountain. *Mammalia* 75: 3–11.
- Kunz, T. H. and A. Kurta. 1988. Capture methods and holding devices. In: *Ecological and behavioral methods for the study of bats*. Smithsonian Institution Press, Washington, DC, USA. pp. 1–29.
- Kunz, T. H., E. Braun de Torrez, D. Bauer, T. Lobova and T.H. Fleming. 2011. Ecosystem services provided by bats. *A. N. Y. Acad. Sci.* 1223: 1–38.
- Kusch, J., C. Weber, S. Idelberger and T. Koob. 2004. Foraging habitat preferences of bats in relation to food supply and spatial vegetation structures in a western European low mountain range forest. *Folia Zool.* 53: 113–128.
- Linden, V. M.G, S.M. Weier, I. Gaigher, H.L. Kuipers, M.J.A. Weterings and P.J. Taylor. 2014. Changes of bat activity, species richness, diversity and community composition over an altitudinal gradient in the Soutpansberg range, South Africa. *Acta Chiropterol.* 16: 27–40.
- Lopez-Gonzalez, C., S.J. Presley, A. Lozano, R.D. Stevens and C.L. Higgins. 2012. Metacommunity analysis of Mexican bats: environmentally mediated structure in an area of high geographic and environmental complexity. *J. Biogeogr.* 39: 177–192.
- McCain, C.M. 2005. Elevational gradients in diversity of small mammals. *Ecology* 86: 366–372.
- McCain, C.M. 2007a. Area and mammalian elevational diversity. *Ecology* 88: 76–86.
- McCain, C.M. 2007b. Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Global Ecol. Biogeogr.* 16: 1–13.
- Mickleburgh, S. P., A.M. Hutson and P.A. Racey. 2002. A review of the global conservation status of bats. *Oryx* 36: 18–34.
- Monadjem, A., P.J. Taylor, F.P.D. Cotterill and M.C. Schoeman. 2010. *Bats of Southern and Central Africa: a biographic and taxonomic synthesis*. Wits University Press, Johannesburg, South Africa. pp. 596+ xii.
- Mostert, T.H.C., G.J. Bredenkamp, H.L. Klopper, C. Verwey, R.E. Mostert and N. Hahn. 2008. Major vegetation types of the Soutpansberg Conservancy and the Blouberg Nature Reserve, South Africa. *Koedoe* 50: 32–48.
- Mucina, L. and M.C. Rutherford. 2006. *The vegetation of South Africa, Lesotho and Swaziland, Strelitzia 19*, South African National Biodiversity Institute, Pretoria, South Africa. pp. 807+ viii.
- Presley, S.J., L.M. Cisneros, B.D. Patterson and M.R. Willig. 2012. Vertebrate metacommunity structure along an extensive elevational gradient in the tropics: a comparison of bats, rodents and birds. *Global Ecol. Biogeogr.* 21: 968–976.
- Rahbek, C. 1995. The elevational gradient of species richness: a uniform pattern? *Ecography* 18: 200–205.
- Rahbek, C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. *Ecol. Lett.* 8: 224–239.
- R Core Team. 2014. *The R project for statistical computing*. Published at: <https://www.r-project.org/>.
- Rosenzweig, M.L. 1992. Species diversity gradients: we know more and less than we thought. *J. Mammal.* 73: 715–730.
- Russo, D. 2002. Elevation affects the distribution of the two sexes in Daubenton's bats *Myotis daubentonii* (Chiroptera: Vesperilionidae) from Italy. *Mammalia* 66: 543–551.
- Sanders, N.J. and C. Rahbek 2012. The patterns and causes of elevational diversity gradients. *Ecography* 35: 1–3.
- Sanders, N.J., J. Lessard, M.C. Fitzpatrick and R. R. Dunn. 2007. Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. *Global Ecol. Biogeogr.* 16: 640–649.
- Sape, T. 2011. *Bat diversity, activity and habitat use at Lajuma, Soutpansberg Mountains*. Unpublished Honours Dissertation, University of Venda, South Africa. pp. 36.
- Taylor, P.J., A. Munyai, I. Gaigher and R. Baxter. 2015. Afromontane small mammals do not follow the hump-shaped rule: elevational variation in a tropical biodiversity hotspot (Soutpansberg Mountains, South Africa). *J. trop. Ecol.* 31: 37–48.

- Taylor, P.J., S. Sowler, M.C. Schoeman and A. Monadjem. 2013. Diversity of bats in the Soutpansberg and Blouberg Mountains of northern South Africa: complementarity of acoustic and non-acoustic survey methods. *South African J. Wildl. Res.* 43: 12–26.
- Terborgh, J. 1973. On the notion of favorableness in plant ecology. *Am. Nat.* 107: 481–501.
- Terborgh, J. 1977. Bird species diversity on an Andean elevational gradient. *Ecology* 58: 1007–1019.
- Thomas, C.D., A. Cameron, R.E. Green, M. Bakkenes, L.J. Beaumont, Y.C. Collingham, B.F.N. Erasmus, M. Ferreira de Siqueira, J. Grainger, L. Hannah, L. Hughes, B. Huntley, A.S. van Jaarsveld, G.F. Midgley, L. Miles, M.A. Ortega-Huerta, A. Townsend Peterson, O.L. Phillips and S.E. Williams. 2004. Extinction risk from climate change. *Nature* 427: 145–148.
- Time and Date AS. 2014. Sun & Moon. Sunset and moonrise in Pretoria. Published at: <http://www.timeanddate.com/>.
- UNESCO. 2010, MAB Biosphere Reserves Directory, Biosphere Reserve Information, South Africa, Vhembe. Published at: <http://www.unesco.org/>.
- Ver Hoef, J.M. and P.L. Boveng. 2007. Quasi-poisson vs. negative binomial regression: How should we model overdispersed count data? *Ecology* 88: 2766–2772.
- Wang, G.H., R.D. Owen, C. Sanchez-Hernandez and M. Romero Almaraz. 2003. Ecological characterization of bat species distributions in Michoacán, México, using a geographic information system. *Global Ecol. Biogeogr.* 12: 65–85.
-
- Supplemental Material:** The online version of this article (DOI: 10.1515/mammalia-2015-0055) offers supplementary material, available to authorised users.