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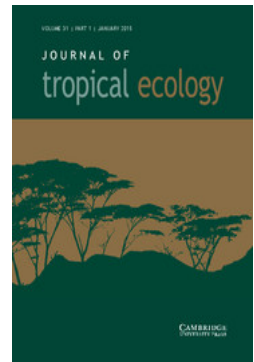
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Afromontane small mammals do not follow the hump-shaped rule: altitudinal variation in the Soutpansberg Mountains, South Africa

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Abstract: Altitudinal transects of biodiversity are important to understanding macro-ecological patterns. Hump-shaped altitudinal profiles in species richness are a common pattern in terrestrial small-mammal communities studied previously mostly in New World mountain ranges. Based on capture–mark–recapture live-trapping conducted over four seasons (four nights per session) along an altitudinal transect from 1000 to 1747 m asl on the southern slopes of the Soutpansberg Mountains of northern South Africa, we recorded 12 species of small mammal, including nine rodents, two shrews and one elephant shrew (sengi). Three species of rodent and the sengi dominated the communities whilst six species were recorded with three or fewer captures. Although we found no effect of season, we found a significant linear increase in terrestrial small-mammal richness (but not Simpson's diversity, D) with altitude in the Soutpansberg Mountains located just north of the Tropic of Capricorn in South Africa. This trend could best be explained by an increase in the proportion of rocky cover and a change in vegetation from savanna to grassland. Peak densities of three common rodent species and one common insectivore varied from 10 ha^{-1} (*Elephantulus myurus*) to 54 ha^{-1} (*Micaelamys namaquensis*) and density showed no significant variation with season. However, density either declined (*Aethomys ineptus*) or increased (*Rhabdomys dilectus* and *Elephantulus myurus*) significantly with altitude; this variation was best explained by the proportion of rocky cover. Seasonal variation had a significant effect on body mass of two rodent species. A review of small-mammal studies from major mountain ranges in Africa and Madagascar found that the hump-shaped pattern is not common. Declines in richness with increasing altitude as well as cases of no significant altitudinal change were the most common patterns noted. Tropical African mountains (including the Soutpansberg with 27 species) have far higher small-mammal diversity than temperate African mountains.

Key words: abundance, Africa, altitude, Bergmann's Rule, habitat, rodents, sengis, shrews, species richness

INTRODUCTION

Mountains contain spatially compressed environmental gradients and associated diverse regional faunas and floras, making them natural laboratories for altitudinal studies that can elucidate past, present and future determinants of diversity. Studies investigating the relationship between species richness and altitude have yielded diverse patterns. Prevalent patterns globally include either a decrease in richness with altitude or a mid-elevation peak, i.e. a hump-shaped pattern

(McCain 2007a, Rahbek 1995). The latter has been shown to be ubiquitous in non-volant small mammals (Brown 2001, McCain 2005, Rowe 2009). A variety of mechanisms have been proposed to explain hump-shaped patterns, from spatial hypotheses such as the mid-domain effect, MDE (Colwell & Lees 2000, Colwell *et al.* 2004, Jetz & Rahbek 2001, McCain 2004, 2005, 2007a) to climatic hypotheses (Kryštufek *et al.* 2011, McCain 2007b, Williams *et al.* 2010) and historical evolutionary filters (Clausnitzer & Kityo 2001, Colwell & Rangel 2010, Heaney *et al.* 1989, Williams *et al.* 2010). Based on 13 rodent studies, Mena & Vázquez-Domínguez (2005) showed that beta-diversity (species turnover) was also highest at mid-elevations.

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At the local scale, factors such as vegetation structure, habitat complexity and disturbance (e.g. successional effects of fire in grassland ecosystems) have been shown to be important determinants of small-mammal community structure changes along altitudinal gradients (Clausnitzer & Kityo 2001, Curran *et al.* 2012, Denys *et al.* 2009, Goodman & Rasolonandrasana 2001, Happold & Happold 1992, Kok *et al.* 2012, Kryštufek *et al.* 2011, Linden *et al.* 2014, Mulungu *et al.* 2008, Patterson *et al.* 1998, Rowe-Rowe & Meester 1982).

The Soutpansberg Mountains of northern South Africa run from west to east for some 210 km, rising above the flat landscape of the Limpopo Valley and ranging in altitude from approximately 800–900 m asl to the highest peak of 1748 m asl. Although not reaching the maximum altitude (>3000 m) found in the Drakensberg Range to the south, neighbouring mountain ranges of similar altitudinal range are found to the west (Blouberg), south (Waterberg) and north-east (Eastern Highlands of Zimbabwe). Biologically rich, the Soutpansberg represents a southern African centre of plant endemism located just north of the Tropic of Capricorn and having a high diversity of plants (>1000 genera and >3000 species) and animals (Berger *et al.* 2003, Foord *et al.* 2008, Hahn 2002, Linden *et al.* 2014, Munyai & Foord 2012, Taylor *et al.* 2013, Van Wyk & Smith 2001). Previous altitudinal transects of the western Soutpansberg have revealed a hump-shaped pattern in ant richness on northern slopes contrasting with a peak at lower altitudes on the southern slopes (Munyai & Foord 2012) as well as a significant decrease with altitude in richness and diversity of bats on the southern slopes (Linden *et al.* 2014).

Based on altitudinal patterns of small-mammal diversity found worldwide we hypothesize a hump-shaped pattern of species richness. Given the uniqueness of Bergmann's Rule we predicted that body size of species widespread across a range of altitudes would repond positively to altitude (Yom-Tov & Geffen 2011, Yom-Tov *et al.* 2006, 2010). Finally, due to reasonably marked seasonal differences in rainfall, and to a lesser extent temperature, we predicted that season would have a significant effect on abundance, diversity and body size.

METHODS

Study site

The Luvhondo Nature Reserve located in the southern aspect of the western part of the Soutpansberg range, Limpopo Province, has an area of about 5000 ha (Figure 1). During the course of the present study between August 2010 and June 2011 (11 mo), total rainfall of between 587 mm (at 1600 m asl) and 849 mm (at

1200 m asl) (mean of 689 mm) was recorded at different trapping sites, with distinct peaks recorded in January 2011 (mean of 249 mm) and April 2011 (mean of 159 mm). A weather station on the Lajuma Research Centre, within the reserve, recorded temperatures varying between 6.3 °C and 36.7 °C in the warm wet season and 4.6 °C and 30.9 °C in the cool dry season. Based on iButtons deployed at each trapping site, mean monthly temperatures for the duration of the study ranged from 15.9 °C at 1747 m asl (ranging from –0.4 °C to 29.6 °C) to 19.4 °C at 1000 m asl (ranging from 3.9 °C–39.9 °C).

The reserve ranges in altitude from 800 to 1748 m asl and is made up mostly of sandstone and quartzite with small patches of basalt. There are several permanent streams and wetlands located within the nature reserve.

Trapping

Permanent trapping grids were set at five different altitudinal sites, namely 1000 m (23.0503°S, 29.46917°E), 1200 m (23.0493°S, 29.44722°E), 1400 m (23.03438°S, 29.43088°E), 1600 m (23.02258°S, 29.43388°E) and 1747 m asl (23.25°S, 29.42917°E). Traps were set in Soutpansberg mountain bushveld (1000–1400 m asl) and Soutpansberg summit sourveld (1600–1747 m asl) (Mucina & Rutherford 2006; Figure 1). The sampling sites were chosen so that they had the same substrate, namely rocky areas. The extent of rock cover increased with increasing altitude. Forty-nine aluminium folding Sherman traps were placed 10 m apart on 7 × 7-fixed grids at each sampling site. Following Massawe *et al.* (2011), allowing for a 5-m buffer strip around the grid to account for short-term dispersal, our grid plots covered an area of 0.49 ha (rounded to 0.5 ha given imprecision in estimating rodent densities). The Sherman traps were baited with oats mixed with cooking oil and checked early in the morning and late in the afternoon.

Sampling at each of the five sites covered four nights per session and was repeated for four consecutive seasons leading to a total of 80 trapping nights (warm dry season: 29 August–3 October 2010; early warm wet season: 25 November 2010–3 February 2011; late warm wet season: 1 April–1 May 2011; cool dry season: 2–13 June 2011).

A permit to sample small mammals was obtained from the Limpopo Department of Environmental Affairs and Tourism (LEDET), Permit No. 001-CPM403–00010. Capture and handling followed the guidelines prescribed by the American Society of Mammalogists (Sikes, Gannon and the Animal Care and Use Committee 2011). Captured individuals were marked by fur-clipping so that they could be recognized when recaptured during subsequent sampling periods. Individuals were weighed using a

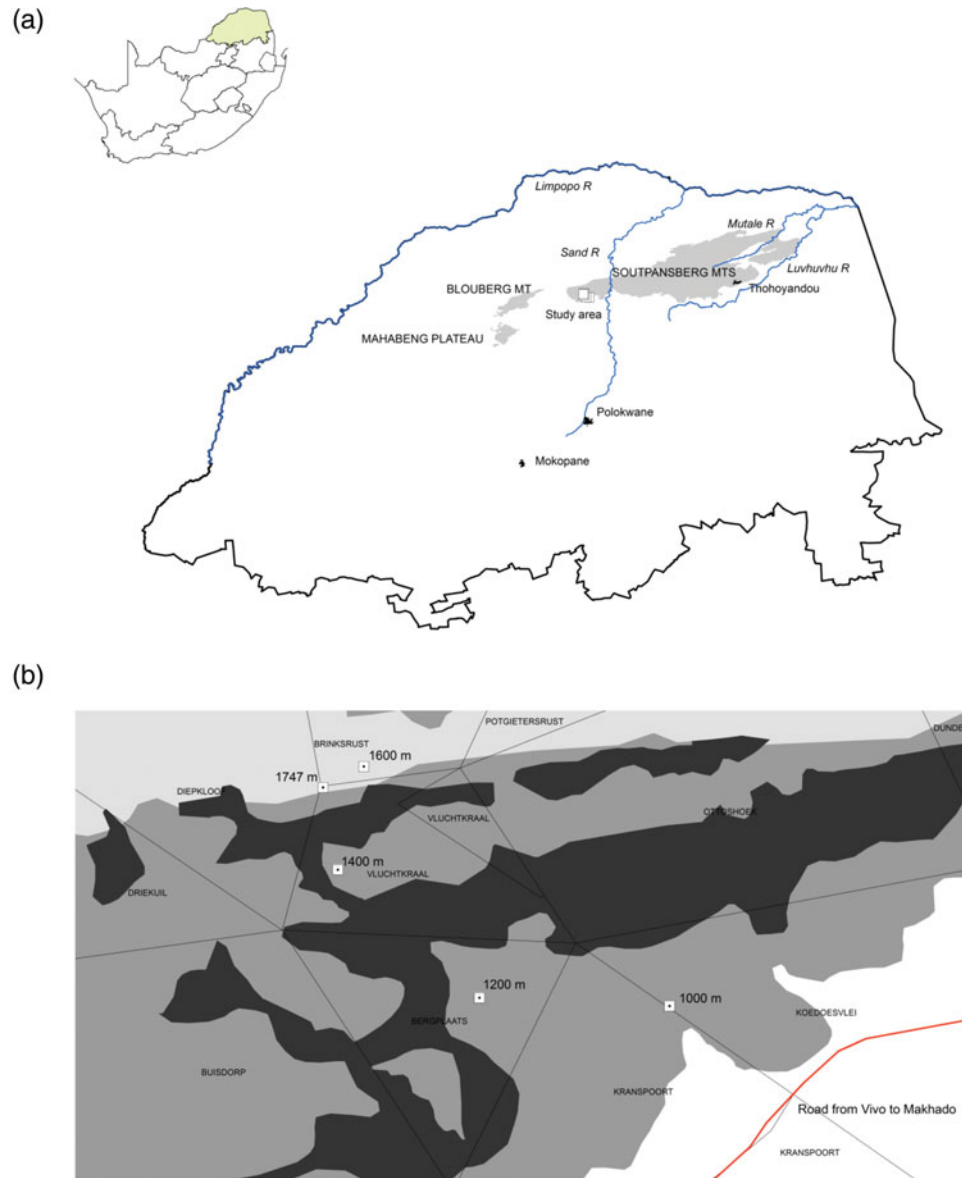


Figure 1. Map showing the location of the Luvhondo Private Nature Reserve in Limpopo Province of South Africa (a) and a detailed vegetation map with farm boundaries included, showing the location of the five altitudinal sites (b). Vegetation types (from Mucina & Rutherford 2006) are indicated as follows: dark grey = Northern Mistbelt Forest; mid-grey = Soutpansberg Mountain Bushveld; light grey = Soutpansberg Summit Sourveld; white = Makhado Sweet Thornveld.

100-g Pesola spring balance with 1-g precision. Species were identified in the field by external characteristics using the key of Newbery (1999). Individuals which could not be identified with certainty in the field were euthanized and prepared as voucher specimens (skulls, skins and/or bodies stored in 70% ethanol), and lodged with the Durban Natural Science Museum. Recent literature and Monadjem *et al.* (in press) was consulted for current nomenclature. *Rhodomys* from the Soutpansberg Mountains has been identified as *R. dilectus*, a species distinct from *R. pumilio* (Castiglia *et al.* 2012, Du Toit

et al. 2012, Monadjem *et al.* in press). *Dasymys* from northern South Africa has been identified as *D. robertsii* distinct from *D. incomtus* (Mullin *et al.* 2005). *Aethomys chrysophilus* was identified from cytochrome-b sequences (C. Chimimba, unpubl. data) based on a single specimen collected during this study from 1600 m. This specimen was one of six *Aethomys* individuals sequenced from the study area; all other specimens were identified as *A. ineptus*. The Soutpansberg is clearly a contact zone between these two cryptic species as suggested by distribution maps in Linzey *et al.* (2003). As the two

cryptic species cannot be identified in the field and as most *Aethomys* specimens were released in our study, we could not distinguish the two species and they were treated as one for the purposes of analysis. Based on Taylor *et al.* (2009) and Engelbrecht *et al.* (2011) we used the name *Otomys auratus* for Limpopo populations. We follow Lecompte *et al.* (2008) and Monadjem *et al.* (in press) in including *namaquensis* in the genus *Micaelamys* and not *Aethomys*.

Habitat and environmental variables

At each of the 49 Sherman traps a 5 × 5-m quadrat was laid. In each quadrat five microhabitat variables (plant height, % leaf litter, % bare soil, % rock cover, % canopy cover) were measured, following Williams *et al.* (2002) and Monadjem (2005).

Shade temperature (mean, minimum and maximum monthly) was measured from August 2010 to June 2011 using Thermocron iButtons/data loggers attached to 1-m poles. Cold chain Thermodynamics software was used to download temperature data from data loggers. Monthly rainfall was recorded at each study site from August 2010 to June 2011 using rain gauges. Additional climatic data, including rainfall and temperature, was obtained from weather stations located at 1200 m and 1747 m asl. These weather stations were placed and monitored by the South African Environmental Observation Network (SAEON).

Data analysis

Small-mammal density was calculated as the minimum number of unique individuals known to be alive (i.e. excluding fur-clipped recaptures) per 7 × 7 trapping grid (approximately 0.5 ha). The statistical software Estimate-S (Version 8.2.0) was used to generate individual-based rarefaction (or species accumulation) curves as well as observed and expected values for small-mammal species richness at each sample session and site. Two richness estimators Chao 2 and Jackknife2 were selected because they are less biased to small samples. Estimate-S (Version 9.1.0, Robert K. Colwell, University of Connecticut, USA) was also used to calculate Simpson's (D) diversity index (Gotelli & Colwell 2001, Magurran 2004).

In order to test the mid-domain effect (MDE), the programme RangeModel (Version 5.0, Robert K. Colwell, University of Connecticut, USA) was used to create a null model for a species saturation curve after 50 000 simulations of empirical species ranges within the altitudinal bounds of the study (Colwell & Lees 2000, McCain 2005). Regression of the empirical values onto predicted values for the 50 000 simulations allowed a test of the fit of our data to the null model.

Using statistical software R 2.11.1 (R development Core Team, Vienna) (www.r-project.org), seven linear regression models were built in trying to test the influence of different spatial and environmental variables on small-mammal species richness, diversity and abundance for 20 sample sessions. Although count data (such as species richness and abundance) often display non-normal distributions and non-constant error variance, necessitating the use of generalized linear models, we tested for normality and non-constant variance by examining the distribution of residuals as well as using the Shapiro–Wilk normality test and the Breusch–Pagan test for non-constant error variance. In all variables, these tests were not significant ($P > 0.05$), justifying the use of linear models. The models tested the influence of several predictor variables including spatial effects (the mid-domain effect), altitude, season, vegetation type, climate (rainfall and temperature) and micro-habitat variables (grass cover, grass height, shrub cover, shrub height, tree cover, tree height, litter cover, rock cover). Initial analyses included all microhabitat variables but, due to high numbers of zero values and/or collinearity between variables, singularities resulted in the regression models making it impossible to calculate coefficients. For this reason, and because exploratory analyses showed no association with independent variables, we removed all microhabitat variables except for percentage of rock cover, which did not display statistical problems and which was shown to be an important determinant of species richness. Akaike's information criterion (AIC) was calculated and used to assess the best model that explained the drivers of species richness (both estimated and observed richness), diversity and abundance. The best model was shown by lowest AIC values (Symonds & Moussalli 2011). We also computed AICc scores as these are more robust at smaller sample sizes.

Changes in body mass due to season and altitude were analysed using two-way ANOVAs to test for differences in altitude (as a factor variable) and season in four species which occurred in multiple altitudes and seasons (*A. ineptus*, *M. namaquensis*, *R. dilectus* and *E. myurus*). One-way ANOVA was used to test for significant variation in mass between seasons in *A. spinosissimus*, which was found only at 1000 m.

RESULTS

After 3920 trap nights, a total number of 701 captures for 498 unique individuals belonging to nine species of rodent, two shrew species and one elephant shrew species were sampled (Table 1). Overall trap success (including recaptures) was high (18%) and varied from 13% at 1000 m to 22% at 1600 m (Table 1).

Table 1. Small-mammal species composition from five altitudinal samples in western Soutpansberg (Luvhondo Private Nature Reserve), indicating minimum number of individuals known to be alive (i.e. excluding recaptures) for 12 small-mammal species sampled over four consecutive seasons. Asterisk indicates identification based on DNA sequences only; since this species cannot be distinguished in the field from *A. ineptus*, records were combined for the purpose of all analyses.

Species	Altitude (m)					Total
	1000	1200	1400	1600	1747	
Order Rodentia						
<i>Aethomys ineptus</i>	23	34	7	4	3	70
<i>Micaelamys namaquensis</i>	29	49	72	46	33	229
<i>Acomys spinosissimus</i>	18	0	0	0	0	18
<i>Dendromus melanotis</i>	1	0	0	0	0	1
* <i>Aethomys chrysophilus</i>	0	0	0	1	0	1
<i>Rhabdomys dilectus</i>	0	1	9	74	55	137
<i>Otomys angoniensis</i>	0	0	0	1	1	2
<i>Graphiurus murinus</i>	0	0	0	0	1	1
<i>Paraxerus cepapi</i>	0	0	4	0	0	3
Order Eulipotyphla						
<i>Myosorex varius</i>	0	0	1	0	5	5
<i>Crocidura maquassiensis</i>	0	0	0	2	0	2
Order Macroscelidea						
<i>Elephantulus myurus</i>	0	0	6	17	6	29
Total number of individuals	71	84	99	144	104	498
Total number of captures (including recaptures)	100	137	147	176	141	701
Total number of species	4	3	5	6	7	12
Estimated richness (Chao2)	4.0 ± 0.4	3.0 ± 0.3	5.0 ± 0.42	6.0 ± 0.16	9.0 ± 3.74	
% completeness of sample	100	100	100	100	78	
Estimated richness (Jack2)	5.8 ± 0.77	4.8 ± 1.04	6.8 ± 0.71	6.2 ± 1.56	9.8 ± 1.55	
% completeness of sample	68	62	73	97	71	
Species diversity (Simpson)	3.1 ± 0.03	2.0 ± 0.03	1.7 ± 0.06	2.6 ± 0.05	2.6 ± 0.06	
Total number of trap nights	784	784	784	784	784	3920
Trap success including recaptures (%)	12.8	17.5	18.8	22.4	18.0	17.9

Population responses to altitude and season

Of the four most widespread species, the three rodents (*Micaelamys namaquensis*, *Aethomys ineptus* and *Rhabdomys dilectus*) showed marked seasonal fluctuations in abundance (density) within altitudinal zones, reaching peak densities of 50 ha⁻¹ (*R. dilectus*), 54 ha⁻¹ (*M. namaquensis*) and 22 ha⁻¹ (*A. ineptus*), whilst the sengi (*E. myurus*) showed more stable population numbers and a peak density (at 1600 m) of around 10 ha⁻¹ (Figure 2). Seasonal peaks in small-mammal abundance for the three most widespread rodents (*M. namaquensis*, *A. ineptus* and *R. dilectus*) were different at different altitudes. For example, in *M. namaquensis*, early warm-wet-season peaks in abundance occurred at the two lowest and the highest altitude whilst late warm-wet-season or cool-dry-season peaks occurred at 1400 m and 1600 m (Figure 2). Abundance of all species combined did not change significantly with altitude, season or any of the other environmental variables (Table 2x). However, in the case of *A. ineptus*, *R. dilectus* and *E. myurus* (but not *M. namaquensis*) abundance (density) was significantly correlated with altitude, leading to a linear decrease (*A. ineptus*) or increase (*R. dilectus*, *A. myurus*) with increasing

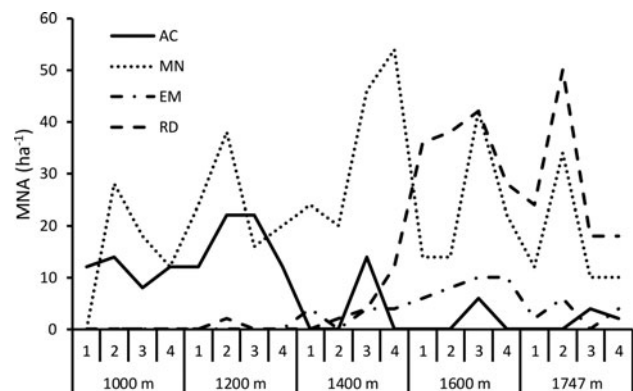


Figure 2. Abundance (Minimum Number Alive: MNA) of most common small mammals at different altitudinal sites over four seasons at Luvhondo Private Reserve in 2010–2011. AC (*Aethomys ineptus*) MN (*Micaelamys namaquensis*); EM (*Elephantulus myurus*); RD (*Rhabdomys dilectus*). Seasons abbreviated as follows: 1 = warm dry; 2 = early warm wet; 3 = late warm wet; 4 = cool dry.

altitude. The model which best explained this relationship in all three cases (lowest AICc) was the one involving the single variable, percentage rock cover (Table 2).

Table 2. Comparison of performance of six regression models testing for environmental predictors of abundance (Minimum Number Alive per 0.5 ha) for all small mammals combined and for the four most common species, over five altitudinal sites in the Soutpansberg Mountains, each sampled in all four seasons ($n = 20$ sample sessions each of four trap-nights). Best models indicated by lowest AICc scores and high adjusted R^2 values. Significance of corresponding ANOVA F-values indicated as * ($P < 0.05$) or ** ($P < 0.01$). In models 1, 2, 4, and 5 single variables were tested. In model 3, four variables were tested and model 6 all eight variables were tested.

Model	All species		<i>Aethomys ineptus</i>		<i>Micaeamys namaquensis</i>		<i>Rhabdomys dilectus</i>		<i>Elephantulus myurus</i>	
	AICc	R^2	AICc	R^2	AICc	R^2	AICc	R^2	AICc	R^2
1. Altitude	156.7	0.11	103.2	-0.45**	140.3	-0.05	129.4	0.6**	75.8	0.36**
2. Season	163.6	-0.008	120.8	-0.06	144.3	-0.03	154.8	-0.15	92.3	-0.17
3. Climate	167.3	-0.05	116.4	0.26	150.3	-0.2	145.7	0.37*	87.0	0.22
4. Vegetation	156.5	0.12	95.2	0.63**	139.4	-0.01	136.8	0.41**	73.0	0.45**
5. Rockiness	155.6	0.16	94.4	0.65**	140.3	-0.005	125.2	0.67**	68.8	0.55**
6. Global	209.5	-0.18	137.2	0.71**	188.2	-0.09	169.8	0.72*	122.1	0.39**

Table 3. Comparison of performance of seven regression models testing for geometrical (mid-domain effect: MDE) and environmental predictors of observed and expected (Jack2) species richness and Simpson's diversity index (D) over five altitudinal sites, each sampled in all four seasons ($n = 20$ sample sessions each of four trap-nights). Best models indicated by lowest AICc scores and high adjusted R^2 values. Significance of corresponding ANOVA F-values indicated as * ($P < 0.05$) or ** ($P < 0.01$). In models 1, 2, 3, 5 and 6 single variables were tested. In model 4, four variables were tested and model 7 eight variables were tested (all other predictor variables except altitude).

	Observed richness		Estimated richness (Jack2)		Simpson's diversity (D)	
	AICc	Adj. R^2	AICc	Adj. R^2	AICc	Adj. R^2
1. Geometry (MDE)	66.8	-0.04	88.2	-0.02	50.6	-0.30**
2. Altitude	52.0	0.50**	66.8	0.65**	57.9	-0.004
3. Season	71.0	-0.03	93.2	-0.05	58.0	0.19
4. Climate	66.6	0.28	84.1	0.42*	65.1	0.003
5. Vegetation types	52.2	0.50**	74.2	0.49**	58.9	-0.005
6. Percentage rock cover	47.5	0.60**	67.8	0.63**	57.2	0.03
7. Global (except Altitude)	96.4	0.57*	112.2	0.68*	86.0	0.61*

Community responses to altitude and season

Season had no significant effect on measures of species richness, diversity and abundance (Tables 2 and 3). The small-mammal community comprised 12 species in total including a number of rarely recorded species occurring at only one or two sites, in addition to three rodent species (*A. ineptus*, *M. namaquensis* and *R. dilectus*) and one insectivore (*E. myurus*) that were abundant and widespread (Table 1). Our study sites occupied two vegetation types from two distinct biomes, with the lower three sites corresponding to Soutpansberg Mountain Bushveld (Savanna Biome) and the upper two corresponding to Soutpansberg Summit Sourveld (Grassland Biome) (Figure 1). As expected, grassland-associated species such as *R. dilectus* and *M. varius* were closely associated with the two upper grassland sites (Table 1). We expected to record the grassland-associated *O. auratus* associated with the grassland site but instead recorded *O. angoniensis*, a species typically associated with wetlands in savanna associations.

Based on individual-based rarefaction curves and estimated richness using the Chao2 and Jackknife2 estimators (Table 1, Figure 3), small-mammal communities at

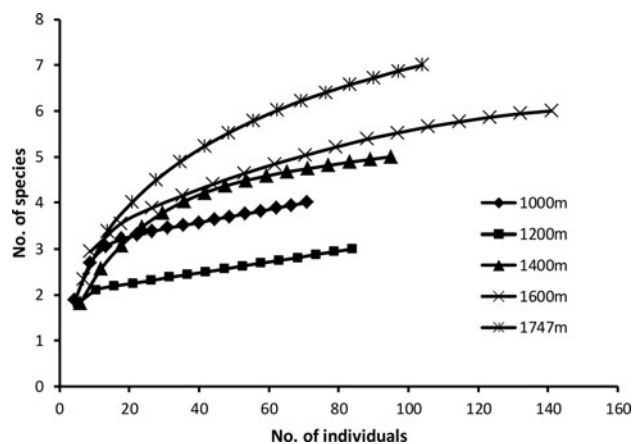


Figure 3. Individual based rarefaction curves of small-mammal species richness for each altitudinal sample for five sites sampled at Luvhondo Private Nature Reserve.

each altitude were fairly well to completely sampled (62–97% for Jackknife2 and 78–100% for Chao2). We found a significant linear increase in both observed and estimated (Jackknife2) species richness with altitude (Table 3, Figure 4a). Simpson's D instead showed a curvilinear,

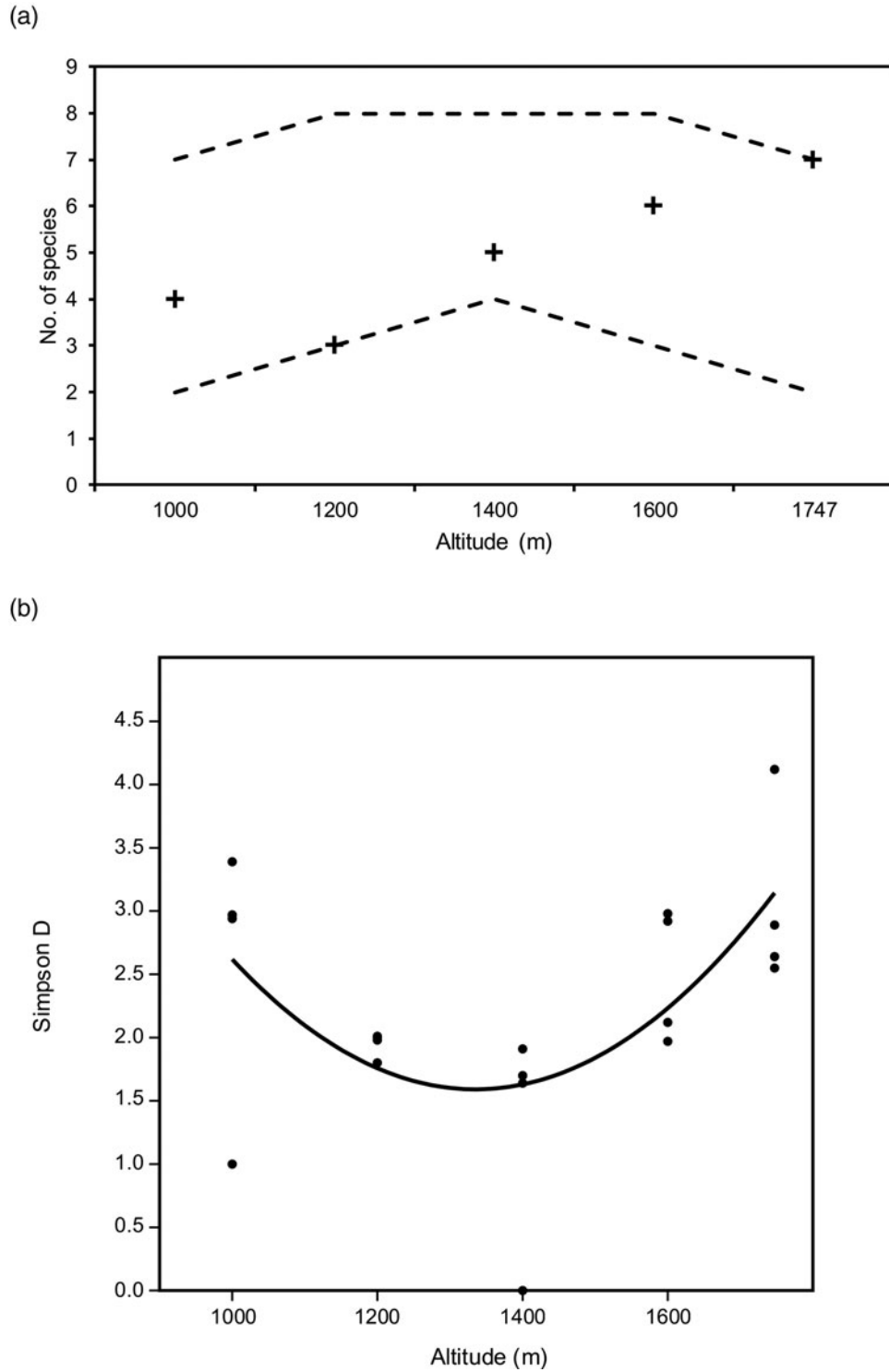


Figure 4. Empirical relationship between altitude and species richness in this study (mean values shown as crosses for each altitudinal site) shown against the predicted species richness based on the Mid-Domain Effect (MDE) estimated from null model with 50 000 replications (dashed lines show 95% confidence limits of the model) (a); Polynomial (quadratic) regression describing reverse hump-shaped relationship between Simpson's diversity (D) and altitude. Points represent four seasonal trapping sessions per site (b). The curve shows the best-fit quadratic relationship ($r^2 = 0.041$; $P = 0.01$) as defined by the equation: $\text{Simpson's } D = 0.000009 (\text{altitude}^2) - 0.0244 (\text{altitude}) + 17.9$.

inverse hump-shaped relationship with altitude, having greatest diversity at both extremes of altitude (Figure 4b: $r = 0.41$, $P < 0.05$). The relationship could be explained by the formula

$$D = (9.15 \times 10^{-6} \times \text{Altitude}^2) - (0.0244 \times \text{Altitude}) + 17.9.$$

The linear increase in observed and estimated (Jackknife2) richness with altitude was best explained (lowest AICc values) by a model comprising just one variable, % rock cover followed closely (slightly higher AICc) by a model involving only vegetation type (Table 3). Observed richness values for each sampled altitude did not follow the hump-shaped pattern predicted by MDE (Table 3: $r^2 = 0.04$, $P > 0.05$). The only predictor variable which was significantly (inversely) correlated with Simpson's D was MDE (Table 3: $r^2 = 0.3$, $P < 0.01$). The expected richness values for MDE produced a hump-shaped altitudinal profile, which was the inverse of the pattern for D which showed an inverse hump-shaped relationship with altitude (Figure 4b).

Phenotypic responses to altitude and season

Apart from in the case of *A. ineptus*, where small sample size ($n = 3$) of the 1600-m sample appeared to have resulted in bias due to the inclusion of one small probably sub-adult individual, body mass did not vary significantly with altitude (Table 4). On the other hand, in all four rodent species tested, body weight was consistently highest in the early warm wet season and lowest in the late warm dry season or cool dry season; this relationship was significant in the case of *A. ineptus* and *M. namaquensis* but not *R. dilectus* or *A. spinosissimus*. In the insectivorous *E. myurus*, largest body size was attained in the cool dry season but there was no significant variation between seasons (Table 4).

DISCUSSION

Seasonal variation in abundance, diversity and phenotype

The absence of significant seasonal effects in our study can be attributed to the mild cool season experienced in the study area. However, season had a significant effect on body mass in two rodent species (*M. namaquensis* and *A. ineptus*), resulting in reduced body mass during the dry season period of scarcer food availability relative to the wet season, as found also in the pouched mouse (*Saccostomus campestris*) from northern South Africa (Ellison *et al.* 1993). In the case of the pouched mouse, the cold dry

Table 4. Results of two-way analysis of variance (ANOVA) and one-way ANOVA (for *Acomys spinosissimus*) to test variation in body mass (g) in five small-mammal species due to altitude and season. Significance indicated by * ($P < 0.05$) and ** ($P < 0.01$). df = degree of freedom. Abbreviations: Eww = early warm wet season; Wd = warm dry season; Lww = late warm wet season; Cd = cool dry season; Alt. = altitude (m); adj. = adjusted.

Species	df	F Alt.	F Season	F Alt. × Season	r ² (adj.)	Season (Means rank)		Season (Tukey test)		Alt. (Means rank)	Alt. (Tukey test)
						Eww > Wd	Lww > Cd	(Eww-Wd)**	(Eww-Lww)**		
<i>Aethomys ineptus</i>	11,57	5.27**	8.33**	5.56**	0.46	Eww > Cd > Lww > Wd	Eww > Wd	(Eww-Wd)**	(Eww-Lww)**	1747 > 1400 > 1200 > 1000 > 1600	(1600-1200)* (1600-1400)*
<i>Micelamys namaquensis</i>	18,198	2.21	4.48**	2.22*	0.14	Eww > Wd > Lww > Cd	Eww > Wd > Lww > Cd	(Eww-Lww)**	(Cd-Eww)**	1200 > 1000 > 1747 > 1600 > 1400	(1400-1200)**
<i>Acomys spinosissimus</i>	2,13	-	2.9	-	0.21	Eww > Wd > Lww > Cd	Eww > Wd > Lww > Cd	NS	NS	-	-
<i>Rhabdomys dilectus</i>	3, 111	1.21	2.18	0.39	0.01	Eww > Lww > Wd > Cd	Eww > Lww > Wd > Cd	NS	NS	1200 > 1600 > 1400 > 1747	NS
<i>Elephantulus myurus</i>	3, 18	2.62	0.99	0.03	0.007	Cd > Wd > Eww > Lww	Cd > Wd > Eww > Lww	NS	NS	1747 > 1400 > 1600	NS

season decline in body size was not due to seasonally varying age profiles but due to decline in mean body mass of the younger age classes due to poor nutrition (Ellison *et al.* 1993). This was probably also true for our study as juveniles were very few in number and occurred in all seasons in those two rodent species that showed significant seasonal differences in mass.

Although it has been shown that relative abundance (trap success) of small mammals is generally highest in the late rainy season or early dry season due to recruitment (Avenant & Cavallini 2007, Avenant *et al.* 2008), our data showed that different seasonal peaks in rodent densities occurred at different altitudes, cautioning against generalizations about optimal trapping times.

Altitudinal variation in abundance, diversity and phenotype

Alpha species richness (3–7 species per site) in the current study was comparable with that of other studies conducted at temperate climate sites along the South African Great Escarpment (Kok *et al.* 2012). However, gamma diversity for the Luvhondo Private Nature Reserve in the western Soutpansberg (Munyai 2014, Nemakhavhani 2014, I. Gaigher pers. comm. and records of the Durban Natural Science Museum; 27 species) was much higher than alpha diversity and comparable with the results of surveys conducted in tropical Afromontane regions such as the Cameroon Mountains (17 species: Denys *et al.* 2009), Bale Mountains (19 species: Yalden 1988), Mt Kilimanjaro (20 species: Mulungu *et al.* 2008), Mt Elgon National Park (34 species: Clausnitzer & Kityo 2001), Eastern Arc Range (23 species: Stanley & Hutterer 2007) and Mt Andringitra in Madagascar (27 species: Goodman & Rasolonandrasana 2001), but much lower than that recorded in the Rwenzori Mountains (67 species). The surprisingly high species richness of terrestrial small mammals in the Soutpansberg Mountains mirrors similar findings from the same region in other plants and animals, including bats (Linden *et al.* 2014, Taylor *et al.* 2013) and is probably at least in part due to high habitat heterogeneity resulting from the presence of grassland, forest and savanna biomes as well as strong east-west and north-south environmental gradients. Annual precipitation varies by almost an order of magnitude from just over 300 mm on northern slopes to >3000 mm at Entabeni on the south-eastern slopes (Berger *et al.* 2003).

Our study revealed a significant increase in species richness with altitude, similar to that shown in the Bale Mountains of Ethiopia (Yalden 1988) and (for rodents but not shrews) in the Udzungwa Mountains of the Eastern Arc Range in Tanzania (Stanley & Hutterer

2007). On the other hand, declines in species richness at higher altitudes (usually above the treeline) have been shown in some studies of Afromontane terrestrial small mammals, e.g. in the Cameroon Mountains (Denys *et al.* 2009), Rwenzori Mountains (Kasangaki *et al.* 2003), Mt Elgon (Clausnitzer & Kityo 2001) and Mt Kilimanjaro (Mulungu *et al.* 2008). No discernible altitudinal changes in richness or diversity were detected in the Zomba Plateau of Malawi (Happold & Happold 1992), Drakensberg Mountains (Rowe-Rowe & Meester 1982) or Cape Fold Belt Mountains (Bond *et al.* 1980) of South Africa. A hump-shaped pattern was found at Andringitra Massif of Madagascar (Goodman & Rasolonandrasana 2001). Taken together, these data indicate that contrary to the global trend, hump-shaped altitudinal profiles are rare in Afromontane terrestrial small mammals.

In our study, variation in both abundance and species richness (but not diversity) was best explained by the percentage of rocky cover (rockiness) which increases with altitude. Perhaps because of their complexity and the shelter they provide for both rupicolous and non-rupicolous small mammals, rocky habitats are often found to have greatest abundance and diversity of small mammals (Bond *et al.* 1980, Kok *et al.* 2012, Rowe-Rowe & Meester 1982). In addition, vegetation type was an important determinant of observed and estimated richness, whereby grassland biome habitats (Soutpansberg Summit Sourveld) were significantly richer in smaller mammals than savanna biome habitats (Soutpansberg Mountain Bushveld). Paradoxically, in tropical mountain systems montane and alpine grassland habitats are usually lower in small-mammal richness than the montane and tropical forests which occupy their lower slopes (Clausnitzer & Kityo 2001, Kasangaki *et al.* 2003, Mulungu *et al.* 2008). This explains the predominant pattern of decline in richness with altitude in most Afrotropical studies compared with our results.

Species diversity is often assumed to follow the same pattern as species richness but in our study, species diversity followed an inverse hump-shaped pattern since evenness was reduced at mid-elevations due to domination of captures by *M. namaquensis*.

We expected to find differences in body mass consistent with Bergmann's Rule whereby populations from the highest altitude (lowest temperature) might be expected to be larger-sized than those from lower altitudes having warmer temperatures (Bergmann 1847). The absence of a significant correlation between body mass and altitude in our study may be partly due to the relatively small difference in altitude (1200–1747 m asl) associated with a difference of mean monthly temperature of only about 3.5 °C (from 15.9 °C at 1747 m asl to 19.4 °C at 1000 m asl).

Conclusions and future prospects

Studies of altitudinal patterns in Afromontane small mammals seem to indicate a prevalent pattern of declining richness with altitude due to rich tropical and montane forests occurring on lower slopes and less rich grasslands and moorlands above the treeline. In temperate African studies (e.g. along the Great Escarpment of South Africa), grassland or fynbos habitats tend to prevail throughout all altitudes and altitudinal trends are not apparent; local factors such as the effects of fire seem to play an important role. In the Soutpansberg, savanna habitats prevail on the lower slopes whilst productive and complex grasslands (which include fynbos elements) occur at the summit, resulting in a unique pattern of increasing richness with altitude. The tropical location of the Soutpansberg ensures the occurrence of species such as the giant rat (*Cricetomys gambianus*) which are not found further south, contributing to the relatively higher richness of small mammals from the Soutpansberg compared with studies elsewhere on the Great Escarpment of South Africa.

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LITERATURE CITED

- AVENANT, N. L. & CAVALLINI, P. 2007. Correlating rodent community structure with ecological integrity, Tussen-die-Riviere Nature Reserve, Free State province, South Africa. *Integrative Zoology* 2:212–219.
- AVENANT, N. L., WATSON, J. P. & SCHULZE, E. 2008. Correlating small mammal community characteristics and habitat integrity in the Caledon Nature Reserve, South Africa. *Mammalia* 72:186–191.
- BERGER, K., CRAFFORD, J. E., GAIGHER, I., GAIGHER, M. J., HAHN, N. & MACDONALD, I. 2003. *A first synthesis of the environmental, biological & cultural assets of the Soutpansberg*. Leach Printers & Signs CC, Louis Trichardt. 62 pp.
- BERGMANN, C. 1847. Über die Verhältnisse der Wärmeökonomie der Thiere zu Ihrer Grösse. *Göttinger Studien* 3:595–708.
- BOND, W., FERGUSON, M. & FORSYTH, G. 1980. Small mammals and habitat structure along altitudinal gradients in the southern Cape mountains. *South African Journal of Zoology* 15:34–43.
- BROWN, J. H. 2001. Mammals on mountainsides: elevational patterns of diversity. *Global Ecology and Biogeography* 10:101–109.
- CASTIGLIA, R., SOLANO, E., MAKUNDI, R. H., HULSELMANS, J., VERHEYEN, E. & COLANGELO, P. 2012. Rapid chromosomal evolution in the mesic four-striped grass rat *Rhabdomys pumilio* (Rodentia, Muridae) revealed by mtDNA phylogeographic analysis. *Journal of Zoological Systematics and Evolutionary Research* 50:165–172.
- CLAUSNITZER, V. & KITYO, R. 2001. Altitudinal distribution of rodents (Muridae and Gliridae) on Mt Elgon, Uganda. *Tropical Zoology* 14:95–118.
- COLWELL, R. K. & LEES, D. C. 2000. The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology and Evolution* 15:70–76.
- COLWELL, R. K. & RANGEL, T. F. 2010. A stochastic, evolutionary model for range shifts and richness on tropical elevational gradients under Quaternary glacial cycles. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:3695–3707.
- COLWELL, R. K., RAHBK, C. & GOTELLI, N. J. 2004. The mid-domain effect and species richness patterns: what have we learned so far? *American Naturalist* 163:E1–E23.
- CURRAN, M., KOPP, M., BECK, J. & FAHR, J. 2012. Species diversity of bats along an altitudinal gradient on Mount Mulanje, southern Malawi. *Journal of Tropical Ecology* 28:243–253.
- DENYS, C., MISSOUP, A. D., TCHIENGUE, B., ACHOUNDONG, G., EKOBO, A., BILONG BILONG, C. F., LEMBE, D. M. & NICOLAS, V. 2009. Altitudinal distribution and anthropogenic influence on small mammal assemblages on Mount Kupe, SW Cameroon. *Bonner zoologische Beiträge* 56:159–173.
- DU TOIT, N., VAN VUUREN, B. J., MATTHEE, S. & MATTHEE, C. A. 2012. Biome specificity of distinct genetic lineages within the four-striped mouse *Rhabdomys pumilio* (Rodentia: Muridae) from southern Africa with implications for taxonomy. *Molecular Phylogenetics and Evolution* 65:75–86.
- ELLISON, G. T. H., BRONNER, G. N. & TAYLOR, P. J. 1993. Is the annual cycle in body weight of pouched mice (*Saccostomus campestris*) the result of seasonal changes in adult size or population structure? *Journal of Zoology (London)* 229:545–551.
- ENGELBRECHT, A., TAYLOR, P. J., DANIELS, S. R. & RAMBAU, R. V. 2011. Cryptic speciation in the southern African vlei rat, *Otomys irroratus* complex: evidence derived from mitochondrial cyt b and niche modeling. *Biological Journal of the Linnean Society* 104:192–206.
- FOORD, S. H., MAFADZA, M., DIPPENAAR-SCHOEMAN, A. S. & VAN RENSBURG, B. J. 2008. Micro-scale heterogeneity of spiders (Arachnida: Araneae) in the Soutpansberg, South Africa: a comparative survey and inventory in representative habitats. *African Zoology* 43:156–174.
- GOODMAN, S. M. & RASOLONANDRASANA, B. P. N. 2001. Elevational zonation of birds, insectivores, rodents and primates on the slopes of the Andringitra Massif, Madagascar. *Journal of Natural History* 35:285–305.
- GOTELLI, N. J. & COLWELL, R. K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4:379–391.
- HAHN, N. 2002. *Endemic flora of the Soutpansberg*. University of KwaZulu-Natal, Pietermaritzburg. 219 pp.

- HAPPOLD, D. C. D. & HAPPOLD, M. 1992. The ecology of three communities of small mammals at different altitudes in Malawi, Central Africa. *Journal of Zoology, London* 228: 81–101.
- HEANEY, L. R., HEIDEMAN, P. D., RICKART, E. A., UTZURRUM, R. B. & KLOMPEN, J. S. H. 1989. Elevational zonation of mammals in the central Philippines. *Journal of Tropical Ecology* 5:259–280.
- JETZ, W. & RAHBEK, C. 2001. Geometric constraints explain much of the species richness pattern in African birds. *Proceedings of the National Academy of Sciences USA* 98:5661–5666.
- KASANGAKI, A., KITYO, R. & KERBIS, J. 2003. Diversity of rodents and shrews along an elevational gradient in Bwindi Impenetrable National Park, south-western Uganda. *African Journal of Ecology* 41:115–123.
- KOK, A. D., PARKER, D. M. & BARKER, N. P. 2012. Life on high: the diversity of small mammals at high altitude in South Africa. *Biodiversity and Conservation* 21:2823–2843.
- KRYŠTUFEK, B., DONEV, N. R. & SKOK, J. 2011. Species richness and distribution of non-volant small mammals along an elevational gradient on a Mediterranean mountain. *Mammalia* 75:3–11.
- LECOMPTE, E., APLIN, K., DENYS, C., CATZEFLIS, F., CHADES, M. & CHEVRET, P. 2008. Phylogeny and biogeography of African Murinae based on mitochondrial and nuclear gene sequences, with a new tribal classification of the subfamily. *BMCEvolutionary Biology* 8:199, doi:10.1186/1471-2148-8-199.
- LINDEN, V. M. G., WEIER, S. M., GAIGHER, I., KUIPERS, H. I., WETERINGS, M. J. A. & TAYLOR, P. J. 2014. Changes of bat activity, species richness, diversity and community composition over an altitudinal gradient in the Soutpansberg range, South Africa. *Acta Chiropterologica* 16:27–40.
- LINZEY, A. V., KESNER, M. H., CHIMIMBA, C. T. & NEWBERY, C. 2003. Distribution of veld rat sibling species *Aethomys chrysophilus* and *Aethomys ineptus* (Rodentia: Muridae) in southern Africa. *African Zoology* 38:169–174.
- MAGURRAN, A. E. 2004. *Measuring biological diversity*. Blackwell Science, Oxford. 256 pp.
- MASSAWE, A. W., MULUNGU, L. S., MAKUNDI, R. H., DLAMINI, N., EISEB, S. J., KIRSTEN, F., MAHLABA, T., MALEBANE, P., VON MALTITZ, E., MONADJEM, A., TAYLOR, P., TUTJAVI, V. & BELMAIN, S. R. 2011. Spatial and temporal population dynamics of rodents in three geographically different regions: implication for ecologically based rodent management. *African Zoology* 46: 393–405.
- MCCAIN, C. M. 2004. The mid-domain effect applied to elevational gradient: species richness in Costa Rica. *Journal of Biogeography* 31:19–31.
- 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 diversity? A global case study for bats. *Global Ecology and Biogeography* 16:1–13.
- MENA, J. L. & VÁZQUEZ-DOMÍNGUEZ, E. 2005. Species turnover on elevational gradients in small rodents. *Global Ecology and Biogeography* 14:539–547.
- MONADJEM, A. 2005. Association between avian communities and vegetation structure in low-lying woodland-savanna ecosystem in Swaziland. *Ostrich* 76:45–55.
- MONADJEM, A., TAYLOR, P. J., DENYS, C. & COTTERILL, F. P. D. In press. *Rodents of Sub-Saharan Africa; a biogeographic and taxonomic synthesis*. De Gruyter, Berlin.
- MUCINA, L. & RUTHERFORD, M. C. 2006. *The vegetation of South Africa, Lesotho and Swaziland*. Strelitzia 19. South African National Biodiversity Institute, Pretoria. 807 pp.
- MULLIN, S. K., PILLAY, N. & TAYLOR, P. J. 2005. The distribution of the water rat *Dasymys* (Muridae) in Africa: a review. *South African Journal of Science* 101:117–124.
- MULUNGU, L. S., MAKUNDI, R. H., MASSAWE, A. W., MACHANG’U, R. S. & MBIJE, N. E. 2008. Diversity and distribution of rodent and shrew species associated with variations in altitude on Mount Kilimanjaro, Tanzania. *Mammalia* 72:178–185.
- MUNYAI, A. 2014. *Biodiversity of terrestrial small mammals along an altitudinal transect in the Soutpansberg, Limpopo Province, South Africa*. MSc thesis, University of Venda. 65 pp.
- MUNYAI, T. C. & FOORD, S. H. 2012. Ants on a mountain: spatial, environmental and habitat associations along an altitudinal transect in a centre of endemism. *Journal of Insect Conservation* 16:677–695.
- NEMAKHAVHANI, T. 2014. *Spatial and reproductive differentiation of small terrestrial mammals in a complex environment in the western Soutpansberg Mountain, Limpopo province*. MSc thesis, University of Venda, Thohoyandou, South Africa. 74 pp.
- NEWBERY, C. H. 1999. A key to the Soricidae, Macroscelididae, Gliridae and Muridae of Gauteng, North West, Mpumalanga, and the Northern Province, South Africa. *Koedoe* 42:51–55.
- PATTERSON, B. D., STOTZ, D. F., SOLARI, S., FITZPATRICK, J. W. & PACHECO, V. 1998. Contrasting patterns of elevational zonation for birds and mammals in the Andes of Southeastern Peru. *Journal of Biogeography* 25:593–607.
- RAHBEK, C. 1995. The elevational gradient of species richness: a uniform pattern? *Ecography* 18:200–205.
- ROWE, R. J. 2009. Environmental and geometric drivers of small mammal diversity along elevational gradients in Utah. *Ecography* 32:411–422.
- ROWE-ROWE, D. T. & MEESTER, J. 1982. Habitat preferences and abundance relations of small mammals in the Natal Drakensberg. *South African Journal of Zoology* 17:202–209.
- SIKES, R. S., GANNON, W. L. & THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92:235–253.
- STANLEY, W. T. & HUTTERER, R. 2007. Differences in abundance and species richness between shrews and rodents along an elevational gradient in the Udzungwa Mountains, Tanzania. *Acta Theriologica* 52:261–275.
- SYMONDS, A. R. E. & MOUSSALLI, A. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike’s information criterion. *Behavioral Ecology and Sociobiology* 65:13–21.
- TAYLOR, P. J., MAREE, S., SANDWYK, J., BAXTER, R. & RAMBAU, R. V. 2009. When is a species not a species? Uncoupled phenotypic,

- karyotypic and genotypic divergence in two species of South African laminate-toothed rats (Murinae: Otomyini). *Journal of Zoology (London)* 277:317–332.
- TAYLOR, P. J., SOWLER, S., SCHOEMAN, M. C. & MONADJEM, A. 2013. Diversity of bats in the Soutpansberg and Blouberg Mountains of northern South Africa: complementarity of acoustic and non-acoustic survey methods. *South African Journal of Wildlife Research* 43:12–26.
- VAN WYK, A. E. & SMITH, G. F. 2001. *Regions of floristic endemism in Southern Africa*. Umdaus Press, Pretoria. 199 pp.
- WILLIAMS, S. E., MARSH, H. & WINTER, J. 2002. Spatial scale, species diversity, and habitat structure: small mammals in Australian tropical rain forest. *Ecology* 83:1317–1329.
- WILLIAMS, S. E., SHOO, L. P., HENRIOD, R. & PEARSON, R. G. 2010. Elevational gradients in species abundance, assemblage structure and energy use of rainforest birds in the Australian Wet Tropics bioregion. *Austral Ecology* 35:650–664.
- YALDEN, D. 1988. Small mammals of the Bale Mountains, Ethiopia. *African Journal of Ecology* 26:281–294.
- YOM-TOV, Y. & GEFFEN, E. 2011. Recent spatial and temporal changes in body size of terrestrial vertebrates: probable causes and pitfalls. *Biological Reviews of the Cambridge Philosophical Society* 86:531–541.
- YOM-TOV, Y., YOM-TOV, S., WRIGHT, J., THORNE, C. J. R. & DU FEU, R. 2006. Recent changes in body weight and wing length among some British passerine birds. *Oikos* 112:91–101.
- YOM-TOV, Y., ROOS, A., MORTENSEN, P., WIIG, O., YOM-TOV, S. & HEGGBERGET, T. M. 2010. Recent changes in body size of the Eurasian Otter *Lutra lutra* in Sweden. *Ambio* 39:496–503.