

Elevation filters bat, rodent and shrew communities differently by morphological traits

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Abstract

Aim: Mountains are geographic features that provide sharp elevational gradients which can accommodate a diversity of terrestrial flora and fauna. In the face of climate change, many of these species are being pushed higher to escape ever-increasing temperatures. Despite this, we have little understanding of how species distribute themselves across mountains. African mountains in particular are less studied than mountains elsewhere and the small mammal groups that inhabit them are also poorly studied when compared to other groups. In this study, we examined the responses of three functionally distinct small mammal taxonomic groups to changes in elevation across Africa.

Location: Africa.

Methods: We calculated four functional diversity metrics for 166, 97 and 153 communities of rodents, bats and shrews comprising 225, 183 and 109 species, respectively. We employed RLQ and fourth-corner analyses to identify any associations between the functional traits of the small mammals and elevation and other climatic variables.

Results: We show that the species richness of the three taxa responded differently to increases in elevation, with only rodents showing a mid-elevational hump. The composition of rodent and bat communities differed significantly in upland versus lowland sites, but bat communities showed far more overlap across the elevational gradient. Functional diversity metrics responded differently for each taxon highlighting the importance of using different taxonomic groups when studying elevational patterns of functional diversity.

Main Conclusions: Our study shows that functional divergence increases with elevation in all three taxa, indicating a pervasive and broadly applicable strong environmental filtering at higher elevations. Our findings suggest that species at higher elevations may be at higher risk due to specialization. These species are losing habitat due to ongoing climate change that will force them up the elevational gradient. At the same time, the human population in Africa is predicted to triple in size by the year 2100, which will also likely contribute to further habitat loss and fragmentation. As small mammals often play essential roles in ecosystems, from seed dispersal to soil aeration and predation, understanding the susceptibility of the specialization of species at

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higher elevations is crucial for the effective conservation and management of mountain ecosystems, especially in light of climatic change and human expansion.

KEYWORDS

Afromontane, functional diversity, RLQ analysis, taxonomic diversity, uplands

1 | INTRODUCTION

Mountains are important components of natural landscapes, providing numerous ecosystem services and acting as climate refugia during glaciations (Levinsky et al., 2013; Mengist et al., 2020; Rahbek, Borregaard, Colwell, et al., 2019). They often display gradients in elevation and climatic variables, such as temperature and rainfall (McCain, 2007). Due to this heterogeneity, mountains are useful for testing ecological hypotheses operating at broad geographical scales, where simple manipulative experiments are not feasible.

Variation in species richness along elevational gradients seems to differ according to the two types of mountains (Kohli et al., 2022; McCain, 2007). Wet mountains, those situated in regions receiving high rainfall in the lowlands around the mountain itself, are surrounded by high species richness in the neighbouring lowlands whereas arid mountains are surrounded by low species richness. Moving up the elevational gradient, rainfall tends to decrease in wet regions, while in dry mountains, due to orographic rainfall, it may increase at mid-elevation, creating a “hump-shaped” species richness distribution likely as a direct response to water scarcity (Kohli et al., 2022; McCain, 2007; Rahbek, Borregaard, Colwell, et al., 2019; Weier et al., 2017). Regardless of the ecosystem, the extreme conditions, including large fluctuations in daily minimum and maximum temperatures, at higher elevations, will inevitably curtail species richness at the highest elevations (McCain, 2007).

While patterns of species richness across elevational gradients are widely recognized, the impact of these gradients on functional diversity – the spectrum of traits and ecological roles that species exhibit in a particular ecosystem (Tilman, 2001), is still not fully understood and what knowledge we have is limited to specific taxonomic groups or certain world regions (Chakravarty et al., 2021; Jarzyna et al., 2021). Since the increase in species richness may vary according to different measures of functional diversity, maintaining ecosystem functioning goes beyond studying richness patterns and requires an understanding of how species use their environments. Studying functional diversity can therefore be especially valuable for conservation in mountain systems (Laureto et al., 2015). These areas are known to be of high conservation importance harbouring many rare and threatened species (Farooq et al., 2020). This is particularly true of the Afrotropical mountains (Onditi et al., 2022), which is a globally important region in terms of threatened species (Ceballos & Ehrlich, 2006).

Furthermore, mountains will play an increasingly important role in the long-term persistence of biodiversity in a climatically uncertain future (Payne et al., 2017). With climate predicted to change

significantly over much of Sub-Saharan Africa over the next century (Hulme et al., 2001; Karam et al., 2022), the distributions of species may move up or down mountains as they track suitable habitat shifts (Taylor et al., 2016; Vitasse et al., 2021). Indeed, mountains have been termed ‘escalators to extinction’ as species move higher and higher to flee ever-increasing temperatures (Urban, 2018). As such, it becomes important to be able to predict not just the response of species diversity along an elevational gradient but also the traits of those species, which can be represented as functional diversity (Petchey & Gaston, 2002).

The occurrence of species in a community is determined by both biotic and abiotic factors (Cadotte & Tucker, 2017; Kraft et al., 2015); the former referring to biological interactions such as competition, while the latter specifies environmental variables (Keddy, 1992). These are frequently viewed as ‘filters’ that exclude certain species from a community, and there is continued debate about which determines patterns of species occurrence (Ausprey et al., 2023; Cadotte & Tucker, 2017). Due to the rapid changes in environmental conditions associated with mountains (Graham et al., 2014) environmental filtering plays an important role in elevational gradients (Chakravarty et al., 2021; Onditi et al., 2022), which in turn may affect functional diversity, as only species with specific traits are able to cope with the extreme conditions at high elevations (Montaña-Centellas et al., 2021).

One way to quantify the variation of species' traits along environmental gradients is through varying metrics of functional diversity, which generates values of functional traits of organisms in a given ecosystem, indicating how these differences contribute to ecosystem functioning and biodiversity. However, to effectively study functional diversity it is beneficial to have assemblages comprising many species that may exhibit a wide range of functional traits. African small mammals are therefore an ideal candidate for this analysis since they match the above requirements and have recently been compiled in a freely available dataset (Monadjem et al., 2023). Rodentia (rodents) and Chiroptera (bats) are the two largest orders of mammals globally, and together with the Eulipotyphla (shrews, moles and hedgehogs) account for more than two-thirds of the currently recognized species (Burgin et al., 2018). Despite their relatively smaller size in comparison to larger mammals like carnivores, primates and ungulates, small mammals exhibit a wide range of functional traits. For example, bats are the only mammals with powered flight, while rodents and shrews may include terrestrial, fossorial or arboreal species (Kingdon et al., 2013). Diets also range from insectivorous and carnivorous to frugivorous and nectivorous (Monadjem et al., 2015, 2020). The fact that the African landscape is topographically diverse, with large mountain ranges and uplands bisected by

low-lying valleys and plains (Moucha & Forte, 2011), positions it as an ideal setting for studying patterns of small mammal diversity along elevational gradients.

Furthermore, the fact that communities with unique functional diversity patterns may exist along elevational gradients and that vertebrate occurrence patterns and human settlement in Africa have their highest overlap in montane regions (Fjeldsa & Burgess, 2008), makes this study not only relevant in macroecological terms but also in the context of conservation. In this study, we explore for the first time, the associations between functional diversity and elevation in Sub-Saharan African bats (Chiroptera), insectivores (Soricidae and Macroscelidae) and rodents (Muridae, Nesomyidae and Gliridae). To understand how the environment influences the functional assembly in small mammal communities, we tested which functional traits were linked with climate and elevation. We predicted that for all three groups, species richness will decline with elevation and that their assemblages, due to strong environmental filtering (Chakravarty et al., 2021), will be functionally under-dispersed at higher elevations. Finally, we predicted that flight will result in bat communities being less functionally distinct across altitudes as they possess a greater capacity to move along these gradients.

2 | MATERIALS AND METHODS

2.1 | Study system and species assemblages

This region is topographically varied with uplands above 1600m above sea level scattered across it (Figure 1). Although the continent is not bisected by a single mountain range like the Andes in South America, most of the uplands are situated in southern and east Africa, with central and west Africa considerably flatter by comparison (Figure 1). The largest blocs of uplands include, from south to northeast, the South African highveld, uplands of Namibia and Angola, the Eastern Arc mountains of Tanzania and Kenya, the

Albertine Rift of the DRC, Burundi, Rwanda and Uganda, the uplands of central Kenya and northern Tanzania and the Ethiopian highlands. The Cameroon Volcanic Line is an important, but geographically rather restricted area of upland habitat in central Africa.

2.2 | Data compilation and analysis

We used the assemblages of terrestrial and volant small mammals across Sub-Saharan Africa from the dataset published by Monadjem et al. (2023). This database includes all bats (11 families in the order Chiroptera), all shrews (Soricidae), all sengis or elephant-shrews (Macroscelidae) and rodents in the families Muridae, Nesomyidae and Gliridae. See Monadjem et al. (2023) for a full description of the data and how it was collected. The distribution of the species assemblages across Sub-Saharan Africa for each of the main groups of bats, rodents and insectivores is shown in Figure 1. These sites extend from sea level to >4000m above sea level. Minimum and maximum elevations for the three taxa were: bats, 10–3250m above sea level; rodents: 10–4100m above sea level; and shrews, 10–4050m above sea level. The bat database includes a total of 182 sites comprising 97 species, rodents 224 sites and 166 species and shrews 109 sites and 153 species. For visual presentation, we have arbitrarily categorized elevations into lowland=<500m above sea level; mid-lower=500–1000m; mid-upper=1000–1600m; and uplands=>1600m, but these categories were not used in any analyses. For visualization purposes, we plotted the species richness of each taxon against elevation using the `geom_smooth()` function in `ggplot2`, with `method='lm'`, and fitting a polynomial using `formula=y~poly(x, 2)`.

2.3 | Functional diversity

Functional diversity can be measured in multiple ways (Mammola et al., 2021), although four indices have been suggested as effectively

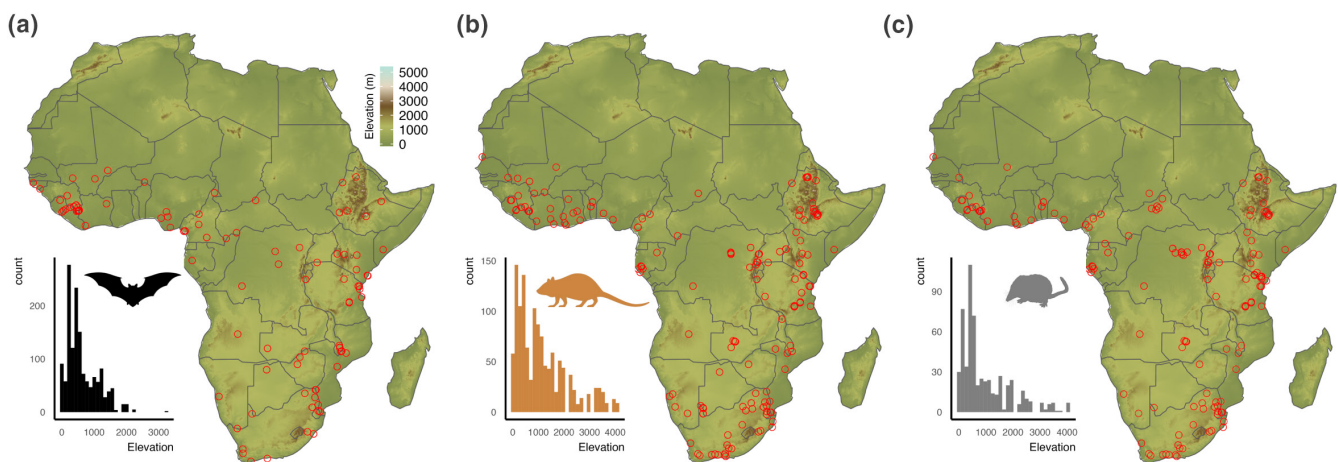


FIGURE 1 Distribution of the species assemblages used in this study shown separately for bats (a), rodents (b) and shrews (c). Inset graphs show the number of records of each small mammal group per elevation category (100m bins) from 0 to 3000m above sea level for bats, and 0 to 4000m above sea level for rodents and shrews.

capturing its important facets namely, Functional Richness (FRic), Functional Evenness (FEve), Functional Divergence (FDiv) and Functional Dispersion (FDis) (Laliberte & Legendre, 2010; Villéger et al., 2008). FRic is the volume of multidimensional trait space that is taken up by the community, with a high value indicating that the community covers a larger volume of multidimensional trait space, meaning that there is a larger diversity of different types of traits available in that community. However, a community comprising a larger number of species will tend to have a larger volume of trait space, and hence FRic is correlated with taxonomic species richness; in contrast, the remaining functional diversity indices do not show such an association. FEve measures how evenly the abundances of species are distributed in trait space, with high values showing that the abundances of individuals with different types of traits are similar, whereas low FEve occurs when species with certain types of traits numerically dominate the community. FDiv emphasizes the separation of species in trait space, with high values indicating a community with extreme values in trait space whereas low FDiv occurs when species are situated close to the centroid of the community, and as such, represents a community composed of species with similar traits. Therefore, a low divergence does not indicate a community of species with similar traits, but rather a community where trait differences between species are less extreme. Finally, FDis is the mean distance of species from the centroid of all species in trait space; however, since this metric essentially expresses the same process as FDiv, we have chosen only to present FDiv in our analyses.

To calculate functional diversity we used both continuous variables (such as measurements of cranial and external features) and factors (arboreal vs. rupicolous rodents or foraging categories of bats)

in our trait matrix (Table 1) obtained from (Monadjem et al., 2023). These features are related to the foraging ecology of each species and are therefore expected to be important in calculating functional diversity (Monadjem et al., 2023). We then calculated three indices for functional diversity: richness (FRic), evenness (FEve) and divergence (FDiv) (Laliberte & Legendre, 2010; Mason et al., 2005; Villéger et al., 2008) using the R package 'FD' (Laliberte et al., 2014), by applying the function dbFD(), without standardization. An important consideration to note with respect to the functional metrics produced by the package FD is that each of these three metrics is calculated using a different method. In particular, functional richness is estimated as the volume of a convex hull, divergence as the distance of the observations to a centre of gravity and evenness with a minimum spanning tree (Laliberte et al., 2014; Laliberte & Legendre, 2010; Villéger et al., 2008). Hence, an important caveat is that our approach may make it difficult to disentangle the effect of the ecological processes from that of the different algorithms used (Mammola et al., 2021).

Some of the continuous traits were relatively highly autocorrelated with other traits, in particular body mass, forearm length (in bats) and head-body length (see Table 1 for definitions, and Table S1 for the correlation coefficients). However, other than the three dental variables, none of the other variables had correlation coefficients greater than 0.95, which may affect functional metrics (Lefcheck et al., 2014). We retained all 10 continuous variables because we felt that they were necessary in describing the functional space of African small mammals. Furthermore, using ordination axes to reduce the dimensionality of functional traits can result in a loss of information (Villéger et al., 2008).

TABLE 1 Trait matrix of morphological and behavioural features used in calculating the functional diversity of African small mammals, based on Monadjem et al. (2023).

Feature	Abbreviations	Type	Bats	Rodents	Shrews
Forearm length (mm)	FA	Continuous	Yes	-	-
Head-body length (mm)	HB	Continuous	Yes	Yes	Yes
Tail length (mm)	TL	Continuous	Yes	Yes	Yes
Ear length (mm)	Ear	Continuous	Yes	Yes	Yes
Hindfoot length (mm)	HF	Continuous	Yes	Yes	Yes
Greatest skull length (mm)	GSKL	Continuous	Yes	Yes	Yes
Skull width at zygomas (mm)	ZYGO	Continuous	Yes	Yes	Yes
Canine to 3rd molar length (mm)	C.M3	Continuous	Yes	-	-
1st molar to 3rd molar length (mm)	M1.M3	Continuous	-	Yes	Yes
Body mass (g)	MASS	Continuous	Yes	Yes	Yes
Foraging assemblage (fruit bat, open air, edge, clutter)	Fruitbat, open. air, edge, clutter	Factor	Yes	-	-
Lifestyle (terrestrial, arboreal, semiaquatic, rupicolous)	Terrestrial, arboreal, semiaquatic, rupicolous	Factor	-	Yes	Yes

Note: For continuous variables, the unit of measurement is provided in parentheses. For factors, their levels are indicated in parentheses.

Abbreviations: Bio15, Precipitation seasonality; Bio18, Precipitation of warmest quarter; Bio19, Precipitation of coldest quarter; MASS, body mass; Bio2, Mean diurnal range of temperatures; Bio3, Isothermality; C.M3, length of the upper tooth row from the canine to the third molar; Ear, ear length; Elevation, elevation above sea level; FA, forearm length; GSKL, greatest skull length; HB, head-body length; HF, hindfoot length; I.M3, length of the upper tooth row from the incisor to the third molar; M1.M3, length of the upper tooth row from the first to the third molar; Tail, tail length; ZYGO, width of skull at the zygomas.

We used linear regression, using the `lm()` function in R, to calculate beta coefficients, test statistics and their significance for the relationship between each functional metric and elevation, for each of the three taxa. We took p values below .05 as indicating beta coefficients that were significantly different from zero.

2.4 | Environmental variables

For our environmental variables, we followed the same workflow as in Monadjem et al. (2023).

We used a subset of 19 variables from the BIOCLIM database (see Table S2 for definitions of the 19 BIOCLIM variables) along with elevation from the WorldClim as our environmental data to which we could relate the species traits. These climatic and elevation variables were at 2.5 min resolution (roughly 4.5 km × 4.5 km across most of the Sub-Saharan African region). This was done for each site where we had occurrences of bats, rodents, or shrews. We assessed multicollinearity among these variables using Variance Inflation Factors (VIFs) which left us with six environmental variables: elevation, BIO2, BIO3, BIO15, BIO18 and BIO19. Their VIF values (range: from 1.39 to 2.18), indicated no multicollinearity. Given that the species data were collected relatively recently (from 1980 onwards), we suggest that the BIOCLIM variables should possess some explanatory power if there is indeed a signal.

2.4.1 | Species composition and environmental variables

We used canonical correspondence analysis (CCA) to identify which environmental variables were associated with the community composition of the three small mammal taxa. CCA is a multivariate analysis that allows assemblages of species to be related to environmental variables (ter Braak & Verdonschot, 1995) and has been used extensively in ecological studies (Borcard et al., 2018); it extracts synthetic environmental gradients from ecological datasets with the assumption of unimodal species relationships (ter Braak & Verdonschot, 1995). In the package `ade4` (Dray et al., 2022), we used the function `'pcaiv'` on the object created by `dudi.coa`, to perform this analysis (Thioulouse et al., 2018).

2.4.2 | Relating traits to environmental variables

We used RLQ analysis to visualize the associations between the small mammal communities and their traits with the environmental variables along the elevational gradient (Dray et al., 2014; Farneda et al., 2015), which we implemented in the R packages `ade4` (Dray et al., 2022). We used RLQ to seek associations between traits and environmental variables, which is accomplished by linking the traits table (named "Q") to the environmental variables table ("R"),

via the species composition table ("L"). The traits table (Q) has trait values (as listed in Table 1) for each of the species of bats, rodents and shrews used in this study, while the environmental table (R) has the climatic variables and elevation (presented in Table S2) for each of the study sites i.e. communities of bats, rodents and shrews (Figure 1). Finally, the species composition table (L) presents the species of bats, rodents and shrews present (or absent) at each of the study sites. Prior to the RLQ analysis, the L (species) table was run through a Correspondence Analysis (CA), while the environmental variables (R) table was run through a Principal Components Analysis (PCA) and the traits (Q) table was run through a Hill and Smith PCA analysis, the latter allowing for the fact that the traits included both continuous variables and factors (Thioulouse et al., 2018).

We then applied fourth-corner analysis (Brown et al., 2014) to test the relationship between the traits of African small mammals and six selected environmental variables (see above), using the function `'traitglm'` in the package `mvabund` (Wang et al., 2012). We set the family of the response variable to binomial with a logit link function because we were modelling the presence-absence of species at sites (i.e., the species composition table contained 1s for presences and 0s for absences). We carried out model selection using LASSO-penalized fits by setting: `'method=glm1path'`. All the statistical analyses were conducted in R v3.3.6 (R Core Team, 2019).

3 | RESULTS

Species richness declined with elevation across all three groups of small mammals, but the exact nature of the decline was different for each group (Figure 2). Bats showed the most extreme declines with bats absent altogether at the highest elevations (>3500m above sea level), where both rodents and shrews were still abundant. The best-fit curve was a polynomial (elevation²) for bats and rodents, but linear for shrews (Figure 2). For bats, mean species richness remained constant until around 500m above sea level, at around 18 species, after which it declined rapidly to just three species above 3000m above sea level. The variation in species richness was visibly large up to about 1500m above sea level, above which it declined rapidly. Rodents showed a hump-shaped relationship, with species richness initially increasing slightly up to 1500m above sea level, where it reached ca. 10 species, and then declining above that, but remain just under 10 species even at 3500m above sea level. The range in species richness remained relatively high throughout the elevational gradient. Shrews gradually and constantly declined with elevation across the entire range sampled in this study, from ca. five species down to three species, with a notable decrease in the variation of species richness up the elevational gradient (Figure 2).

Functional diversity varied by metric and taxon (Figure 3, see Table S3 for beta coefficients and p values). In general, the trend of functional richness along the elevational gradient mirrored that of species richness for all three taxa, declining in bats and shrews, but not for rodents. Functional evenness, and divergence, however, varied between taxa and were generally unrelated to the trends for

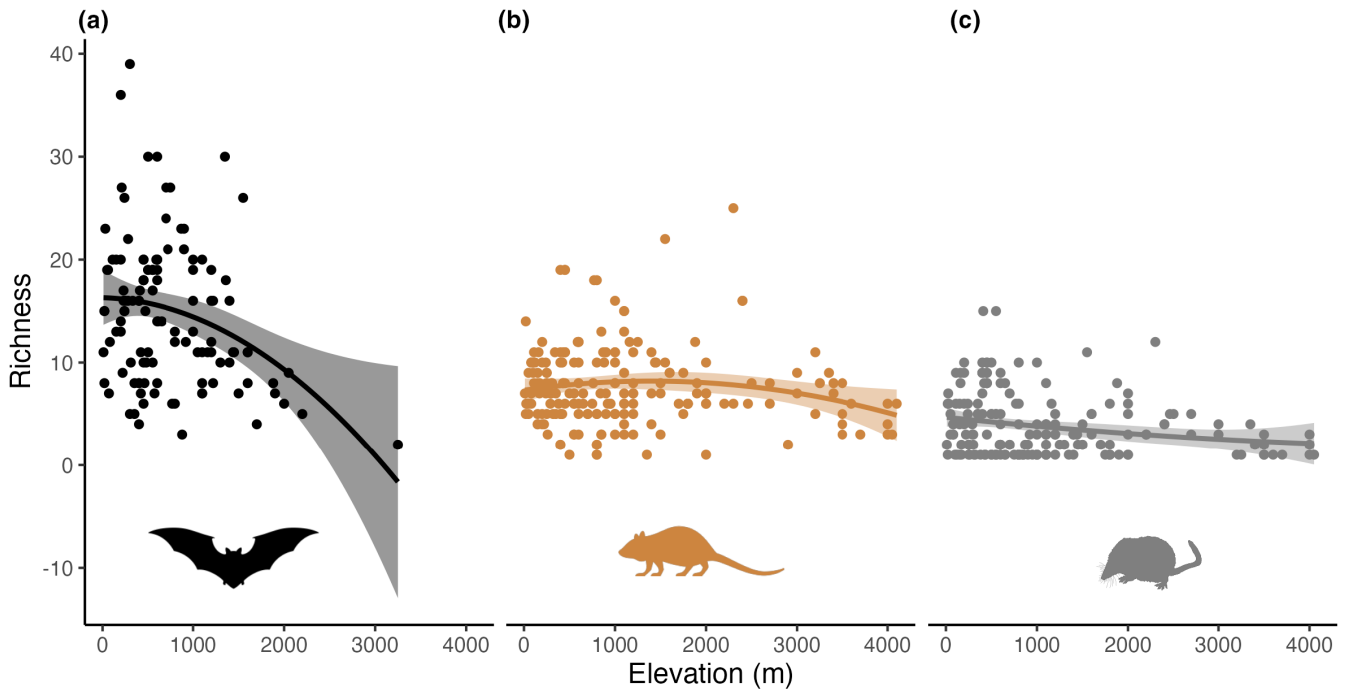


FIGURE 2 Species richness trends with elevation for the three small mammal groups. All three groups show declining species richness with elevation, but with different shaped curves.

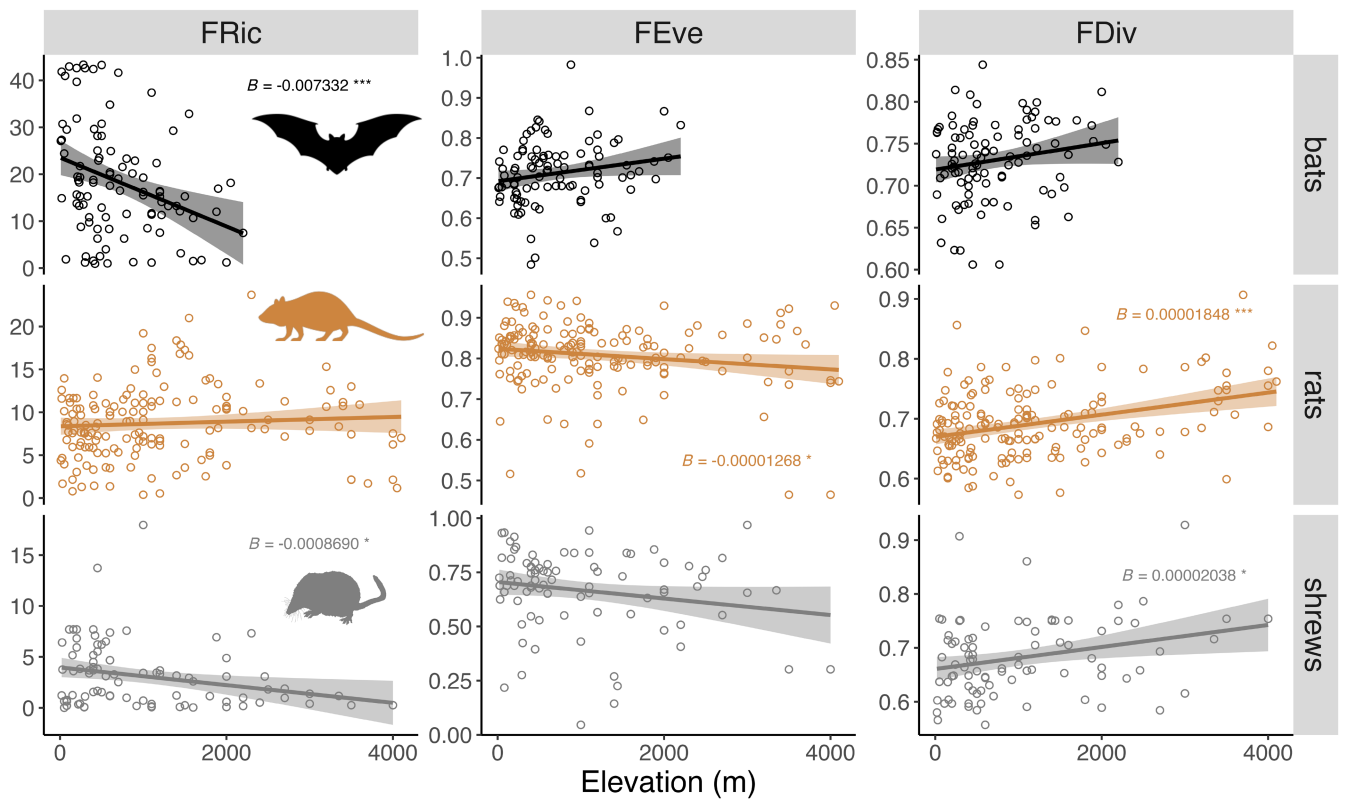


FIGURE 3 Functional diversity metrics for bats (top row), rodents (middle), and shrews (bottom) along an elevational gradient in Sub-Saharan Africa. FDiv, functional divergence; FEve, functional evenness; FRic, functional richness.

species richness. Functional evenness of bats was unaffected by elevation for bats but decreased in both rodents and insectivores.

In contrast, functional divergence increased with elevation in both rodents and shrews.

The CCA separated mammal communities in multidimensional space based on their species composition, but these are also clearly clustered by elevation (Figure 4). This shows that the species composition of all three small mammal communities at higher elevations was distinct from those at lower elevations. The first two axes accounted for 51.8%, 47.0% and 47.1% of the variability for bats, rodents and shrews, respectively. Elevation was strongly correlated with the first axis in shrews but was equally associated with both axes for bats and rodents (Figure 4).

The first two axes of the RLQ analysis explained over 99% of the variance, represented by 89% and 90% of the variance of the environmental variables (table R) for bats (Table 2). In contrast, the first axis explained less of the variance in rodents and shrews, although the first two axes combined explained 94% (Table 2). For bats, the variance of the traits table (Q) was over 97% for both axes, but it was lower in rodents and shrews (Table 2). The species composition table (L) was relatively low for all three taxa (Table 2).

The RLQ analysis showed differences in the clustering of sampling sites for bats compared to rodents and shrews (Figure 5). For

bats, there was significant overlap in sites sampled at different elevations (Figure 5a), with upland sites weakly separating from lower sites on axis 2. The strongest environmental variable associated with axis 2 was Bio2, which is the mean diurnal temperature range (the higher the value the greater the difference between the coldest and warmest part of the day) (Figure 5b). In contrast, the main variables associated with axis 1 were all related to seasonality in both temperature and rainfall (Bio3, Bio15, Bio19) (Figure 5b). Bat species separated relatively well based on the foraging group, with fruit bats clearly separated from the other three foraging groups (Figure 6a). This was associated with differences in functional traits, with fruit bats having larger bodies and shorter tails than other bats (Figure 6b). Cranial dimensions and mass were associated with axis 1, whereas tail and ear lengths were associated with axis 2 (Figure 6b).

These patterns were quite different for rodents, where there was a clear separation between sites based on elevation, with upland sites clustered to the left on axis 1 (Figure 5c). Elevation was strongly associated with this axis (Figure 5d). There were also

FIGURE 4 Biplots of the first two ordination axes of the CCA analysis showing sampling sites (lowland = < 500 m above sea level, mid-lower = 500–1000 m, mid-upper = 1000–1600 m, and uplands = > 1600 m), for African bats (a), rodents (c) and shrews (e). Also shown are the loadings of environmental variables for bats (b), rodents (d) and shrews (f).

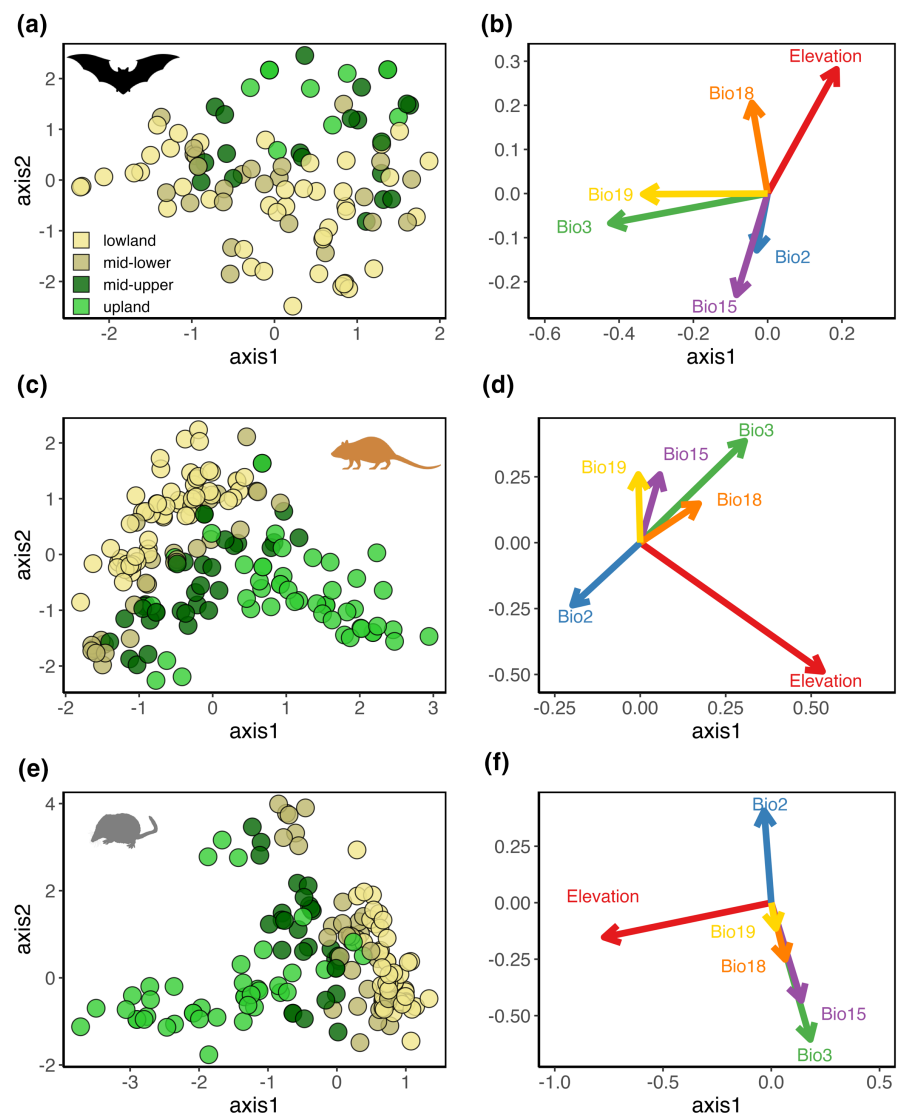


TABLE 2 Results of RLQ analysis between species composition (L), environmental variables (R), and functional traits (Q) for the three African taxa: bats, rodents and shrews.

	Bats		Rodents		Shrews	
	Axis1	Axis2	Axis1	Axis2	Axis1	Axis2
RLQ eigenvalues	0.488	0.007	0.189	0.095	0.214	0.023
Percentage cumulative projected inertia	98.14	99.55	63.11	94.11	85.23	94.27
Projected inertia (% variance) – R	1.89 (89.2)	2.92 (90.2)	1.31 (81.6)	3.42 (95.0)	1.32 (61.7)	2.57 (73.7)
Projected inertia (% variance) – Q	7.11 (97.0)	8.11 (97.9)	5.28 (81.6)	6.74 (92.4)	5.69 (81.1)	6.56 (87.8)
Correlation (% variance) – L	0.19 (22.2)	0.08 (11.9)	0.17 (17.1)	0.18 (18.7)	0.17 (17.0)	0.14 (14.4)

Note: Values presented are for the first two axes of the RLQ analysis.

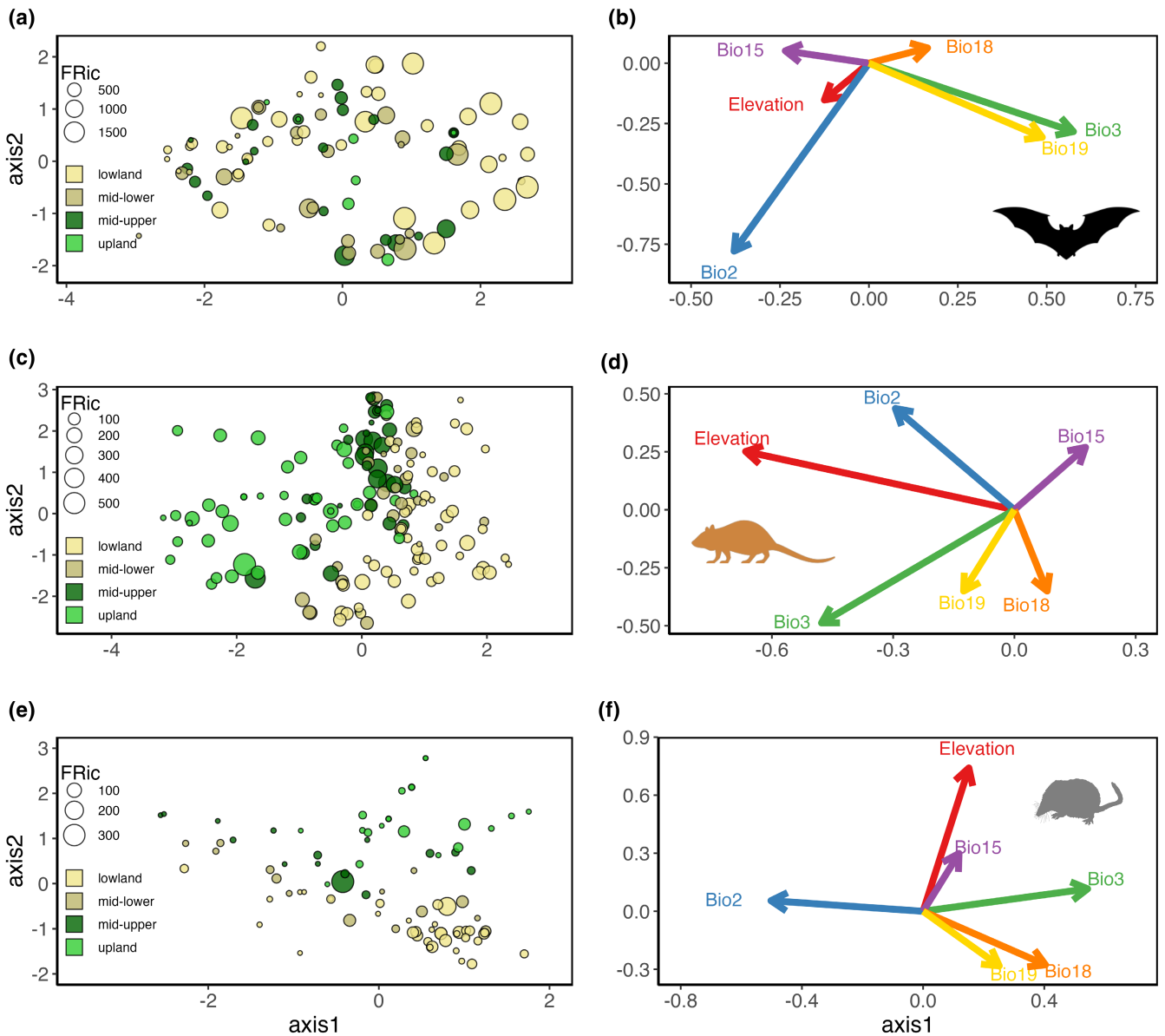


FIGURE 5 Biplots of the first two ordination axes of the RLQ analysis for African bats, rodents and shrews: (a, c and e) sampling sites, with larger circles representing sites with higher FRic (see Figure 3); (b, d and f) loadings of environmental variables.

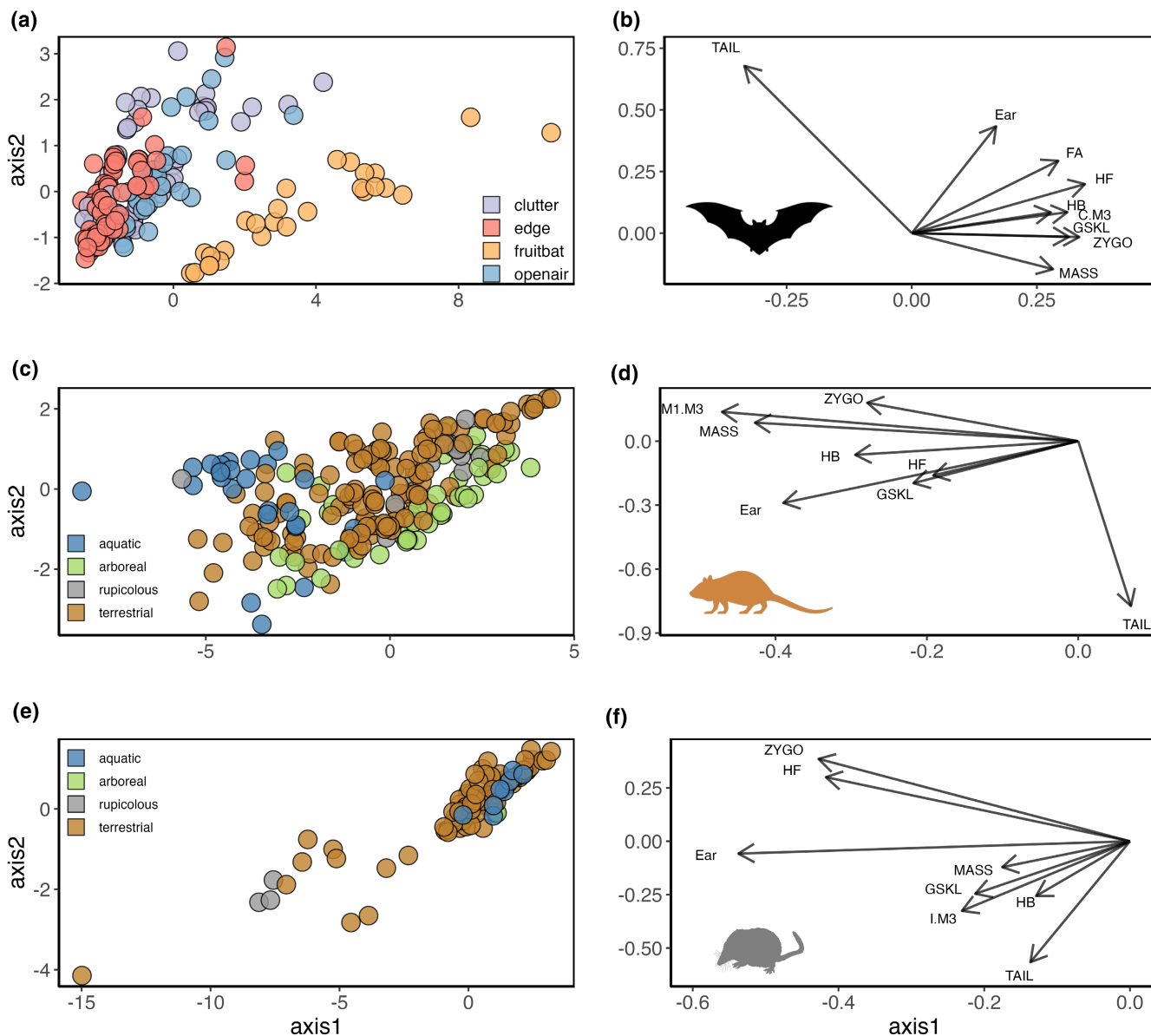


FIGURE 6 Biplots of the first two ordination axes of the RLQ analysis for African bats, rodents, and shrews: (a, c, e) Species categorized by lifestyle/foraging group; (b, d, f) loadings of functional traits.

differences between species based on lifestyle with arboreal species separating from rodents by longer tails and generally smaller size (Figure 6c,d). Water-associated species tended to be larger than others, while there did not seem to be any separation between rupicolous and terrestrial species.

Shrews also showed separation between sites based on elevation (Figure 5e). Upland sites are separated mostly on axis 2 (Figure 5f). There was little separation between shrews based on lifestyle, except that rupicolous species tended to be larger (Figure 6e,f).

The fourth-corner analysis demonstrated many strong interactions between functional traits of all three African small mammal groups and environmental variables (climate and elevation) (Figure S1; Table S4). However, for the most part, the three taxa responded differently. For bats ($\text{pseudo-}R^2 = .106$), the strongest

associations came from isothermality (Bio3, or consistency in temperature fluctuations over the year) which interacted negatively with tail length and positively with hindfoot length (Figure 7a). For rodents ($\text{pseudo-}R^2 = .066$), elevation strongly interacted with tail length (negatively), skull length (negatively), ear length (positively) and length of the upper tooth row from the first to the third molar (positively) (Figure 7b). Finally, for shrews ($\text{pseudo-}R^2 = .152$), there were strong positive interactions between elevation and hindfoot length and zygomatic width, and between Bio18 (precipitation of the warmest quarter) and length of the upper tooth row from the incisor to the third molar (Figure 7c). We note that compared with bats and rodents, shrews showed a greater number of strong interactions (both positive and negative) between functional traits and environmental variables.

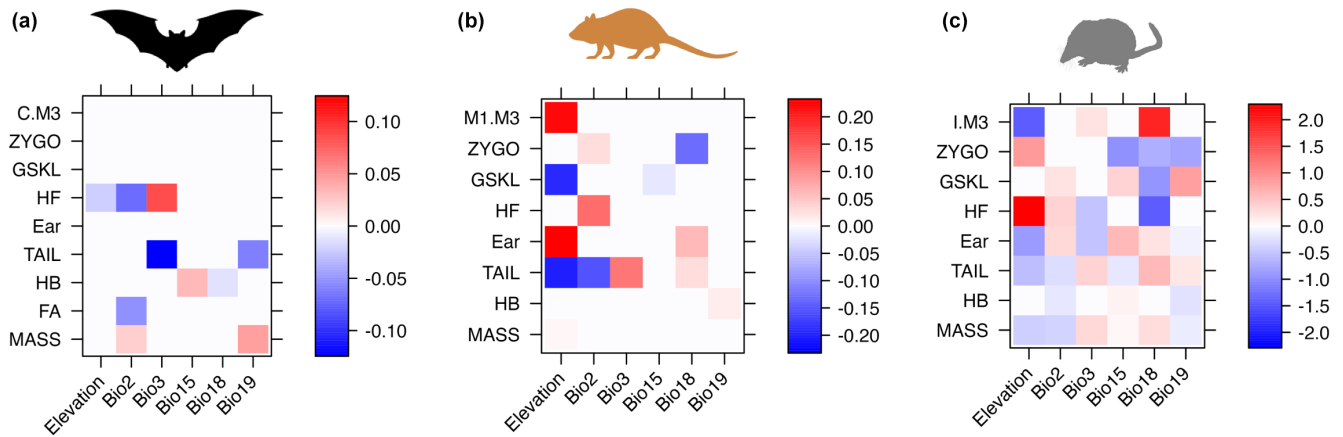


FIGURE 7 The plot of the output of combined RLQ and fourth-corner analysis for bats (a), rodents (b), and shrews (c) relating environmental variables (table R) as columns to functional traits (table Q) as rows. Shaded cells indicate positive (red) or negative (blue) interactions between the functional traits of African bats and environmental variables. The intensity of the shading indicates the strength of association, with darker colours (of either reds or blues) representing stronger associations between the functional trait and the environmental variable. Abbreviations for the functional traits are based on mean values for the species: Bio15, Precipitation seasonality; Bio18, Precipitation of warmest quarter; Bio19, Precipitation of coldest quarter; MASS, body mass; Bio2, Mean diurnal range of temperatures; Bio3, Isothermality; C.M3, length of the upper tooth row from the canine to the third molar; Ear, ear length; Elevation, elevation above sea level; FA, forearm length; GSKL, greatest skull length; HB, head-body length; HF, hindfoot length; I.M3, length of the upper tooth row from the incisor to the third molar; M1.M3, length of the upper tooth row from the first to the third molar; Tail, tail length; ZYGO, width of skull at the zygomas. See text and Table 1 for more information. The coefficients on which these graphs are based are presented in Table S2.

4 | DISCUSSION

In this study, we show continent-wide and taxon-specific associations between small mammal communities and elevation. Furthermore, by combining taxonomic species richness with functional diversity, we have gained greater insights into the patterns and processes that shape biodiversity along an elevational gradient, highlighting the importance of considering both these measures of diversity.

The species richness of bat and shrew communities declined with elevation, albeit in different ways, while species richness for rodents followed a hump-shaped curve, with the highest species richness at elevations of around 1000–2000m above sea level, as reported elsewhere in the tropics (Heaney, 2001; Nor, 2001). This supports the findings of Musila et al. (2019) for species richness of the rodents at Mt Kenya, which also showed a hump-shaped response albeit for only the windward eastern slope. A similar pattern was reported for the higher slopes of the Simien Mountains in Ethiopia (Craig et al., 2020), and Mt Kilimanjaro (Mulungu et al., 2008), although neither of these studies set out to test such relationships. Our continent-wide pattern of rapid decline in bat species richness above ca. 1000m above sea level mirrors that reported from other Afrotropical mountains (Curran et al., 2012; Vogeler et al., 2022; Weier et al., 2017) and elsewhere (Patterson et al., 1996). Furthermore, a critical difference between all the Afrotropical studies and ours, is that our elevational gradient began at sea level, whereas in all the above-mentioned studies, the gradient began at the base of the mountain, which often was already high enough to be considered upland habitat as defined in this study.

The different responses of species richness to elevation by bats and rodents probably relate to the basic biology of these two groups. Rodents in cold climates can escape the worst of the cold by becoming diurnal and sheltering in burrows that are more thermally stable (Cortés et al., 2000; Milling et al., 2018) than the atmospheric conditions that bats would be exposed to. Furthermore, granivorous and herbivorous rodents are more likely to find food on cold mountaintops than insectivorous or frugivorous bats, or insectivorous shrews. This would explain the pattern of the lack of African bats above about 3000m above sea level, whereas rodent communities at this elevation are as species rich as in the lowlands. Similar patterns of rapid reduction of bat species richness at higher elevations appear to be universal for example in southern Mexico (Sánchez-Cordero, 2001), the Andes (Patterson et al., 1996; Presley et al., 2012) and the Himalayas (Chakravarty et al., 2023). Bats do not appear to have been surveyed at higher elevations above 2000m above sea level in South East Asia, but even here, species richness dropped rapidly above about 1500m above sea level (Heaney et al., 1989; Lok et al., 2021). Despite this general trend of precipitous decline in richness at higher elevations, elevations above 3000m in the Andes still harbour 15 species of bats (Patterson et al., 1996), a situation unparalleled in Africa, or possibly elsewhere in the world.

The larger range of species richness at lower elevations (particularly for bats and shrews) compared with upland areas may be explained by either habitat availability and predation (Loggins et al., 2019) or as an artefact of the larger number of studies that have been conducted in the lowlands. In contrast, at higher elevations for all taxa, the almost complete lack of variation in functional

traits is consistent with a strong signal of environmental filtering. We also show that communities of shrews and rodents (and to a far lesser extent of bats) are distinct in species composition at upland sites compared with their lowland counterparts. This points to a unique upland fauna of rodents and shrews, as seen in other tropical mountains (Dreiss et al., 2015). The same pattern was not observed for bats, where there appeared to be a lot of overlap in species composition comparing upland and lowland sites, suggesting that upland bats are a subset of lowland bats (Curran et al., 2012; Presley et al., 2012), rather than a unique upland fauna as in rodents. This points to greater adaptability and habitat usage in bats, perhaps aided by their power of flight.

Functional diversity was also strongly associated with elevation, with rodents and shrews, but not bats, showing higher functional divergence at higher elevations. This again suggests that environmental filters may be playing an important role in structuring the communities of all three taxa living at higher elevations, as has been suggested in the Himalayas (Chakravarty et al., 2021). The extreme climatic conditions and limited resources at higher elevations likely impose strong selective pressures, favouring species with specific traits that enable them to survive and persist under these harsh conditions (Jarzyna et al., 2021). In this way environmental filtering reduces the range of functional traits present in communities at higher elevations, leading to a decline in functional diversity. Environmental filtering has also been implicated in the decline of the functional diversity of birds (Montaño-Centellas et al., 2021) and plants (Ding et al., 2019).

Finally, by applying RLQ and fourth-corner analyses we were able to show clear correspondence between functional traits of these small mammals and environmental variables (specifically elevation and climate). Our analysis identified different sets of traits for bats, rodents, and shrews that were associated with upland environments. Indeed, elevation per se interacts strongly with rodent and shrew trait variables but this is not so for bats. Rodents follow Allen's rule, which posits a positive association between tail length and temperature (Alhajeri et al., 2020), which may explain the relationship we observed in this study between shorter tails at higher elevations. An alternative explanation may be that higher elevations, which are devoid of trees, are unsuitable for arboreal species that have longer tails (Mincer & Russo, 2020), hence a reduction in tail length. Considering that shrews, which are predominantly terrestrial in Africa, did not show a strong negative association between tail length and elevation, suggests substrate (i.e., lack of trees) may be more important than temperature of itself. The pattern of dental traits (larger molars in relation to skull length) of rodents at high elevations corresponds to a shift to a herbivorous diet (Samuels, 2009) in montane regions. A similar pattern has been observed at high elevations in the Andes (Dreiss et al., 2015). For shrews, the relationship between functional traits and upland habitats is primarily a reduction in size, including in overall size (body mass) as well as associated appendages such as tail and ears, together with a reduction in teeth. Perhaps this is driven by nutritional limitations, due to the scarcity of insect food in these extreme environments (Supriya et al., 2019).

In contrast, the positive associations between both hindfoot length and zygomatic width and elevation are puzzling.

Hence, environmental filtering at higher elevations in Sub-Saharan Africa appears to retain terrestrial, herbivorous rodents and tiny-sized shrews. This has important conservation implications under future climate change scenarios. For example, the temperate-associated African herbivorous rodent *Otomys auratus* has disappeared from a South African mountain range, which has been linked to the disappearance of montane grasslands, presumably due to climate change (Taylor et al., 2016). *Otomys* is a diverse African genus of specialist herbivores (Monadjem et al., 2015), many species of which are tied to mountaintop habitats (Taylor et al., 2011), and may thus be similarly impacted by climate change.

We should acknowledge that environmental filtering is a challenging phenomenon to identify because the patterns of community assembly that it produces may also be explained by other processes (Kraft et al., 2015). There are certainly other factors that control small mammal communities beyond environmental filtering including biotic facilitation e.g. seed dispersal, competition for shared resources and dispersal limitations. Then, there are the interactions between biotic and abiotic factors. Kraft et al. (2015) contend that environmental filtering is most likely to occur 'when the species pool is drawn from a broad area containing high abiotic heterogeneity, but the local community is defined to be restricted and abiotically homogeneous'. They also note that one of the first considerations is whether the species in question can disperse to the habitats under study. We suggest that our focus on montane regions works well to assess environmental filtering because they are, in effect, high-altitude regions sampling from a species pool occurring in, often diverse, lowland habitats. Moreover, the vertical distances are typically quite modest such that even small mammals have dispersal distances that exceed them. That said, future work could look to the physiological traits that may ultimately act as the proximate traits that get filtered by the environment to disentangle the drivers of small mammal community assembly (see Byamungu et al. (2021) for a related discussion of the 'physiological tolerance hypothesis' in birds and bats).

The strong associations between community structure and elevation reported here have important implications for the conservation of small mammal communities. Mountains serve both as species pumps, regions that have an increased rates of speciation (Atwood et al., 2020), and climate refugia (Rahbek, Borregaard, Antonelli, et al., 2019). Yet, our results suggest that high-elevation communities may be more vulnerable to environmental changes due to their lower functional diversity, especially for rodents and shrews. Under climate warming, African montane bat communities may be able to extend their range upwards as current unsuitable, colder conditions recede. As many of these communities are currently 'capped' at around 1000m above sea level this represents a viable range shift. However, our focus on functional traits also revealed how African upland sites are home to unique rodent and shrew fauna with specialized traits in contrast to the upland bat communities which are a subset of those at sea level. These specialized groups have no

other habitat to expand into. Thus, rodents and shrews should be the focus of conservation in these regions if we wish to preserve such functional diversity that could not be found elsewhere (Isaac et al., 2007). Under climate warming we can expect to see significant trophic mismatches given the animals and plants that make up the diet of these montane mammal communities are unlikely to respond at the same spatio-temporal scale due to differing thermal preferences (Pintanel et al., 2021). Therefore, 'mediating biotic factors' such as food availability will influence range shifts beyond temperature effects (Neate-Clegg & Tingley, 2023).

Another important conservation consideration is the effect of increased human pressure on these 'sky islands'. As the human population continues to grow in Africa, which is projected to triple by the year 2100, it is likely that many of these mountains will experience increased habitat loss, either due to agricultural expansion and intensification, logging, mining or other anthropogenic activity (Fjeldsa & Burgess, 2008). As we show here, species in these ecosystems appear to be functionally specialized and may be unable to re-colonize new areas putting them at an increased risk. Beyond functional diversity, the genetic diversity within these communities is also crucial for their adaptability and resilience to changing conditions. Having populations of these species extirpated or considerably reduced may have severe snowballing effects on their survival due to genetic resilience and on other species and ecosystems.

In conclusion, our study provides valuable insights into the response of bat, rodent, and shrew communities to elevation in Sub-Saharan Africa. We found that species richness and functional richness declined with increasing elevation, with bats showing the most pronounced decline whereas functional divergence increased in rodents and shrews, a pattern observed on other continents. Our results highlight the specialization of rodent and shrew species at higher elevations due to strong environmental filtering and as a consequence their higher vulnerability to climatic shifts. Understanding the patterns and processes that shape biodiversity along elevational gradients is crucial for the effective conservation and management of mountain ecosystems.

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CONFLICT OF INTEREST STATEMENT

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DATA AVAILABILITY STATEMENT

Data for analysis are available at <https://github.com/kanead/elevation>.

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BIOSKETCH

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Author contributions: A.M. conceived the idea, collected the data and led the analysis and writing of the manuscript. H.F. helped analyse the data and designed the figures. A.K. helped analyse the data. All authors contributed to the drafts of the manuscript.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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