

Strapline: We demonstrated that beta diversity of African small mammals is influenced mostly by spatial distance between sites, which in turn is related to the dispersal ability of the taxon

Dispersal ability is associated with contrasting patterns of beta diversity of African small mammal communities

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AUTHOR CONTRIBUTIONS

A.M. conceived the study and collated all the datasets, K.H. and T.G. prepared the phylogenetic data, A.M. and A.K. analysed the data, A.M. wrote the first draft of the manuscript. All authors discussed the results and provided input on the manuscript.

DATA AVAILABILITY STATEMENT

Data and R code for analysis are available at https://github.com/kanead/beta_diversity

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Abstract

Aim: Spatial processes and environmental filtering are important factors shaping community composition, but their effects are rarely tested across all aspects and components of beta diversity. We investigate both of these factors to explain patterns of taxonomic, functional, and phylogenetic beta diversity of small mammals across Sub-Saharan Africa. We predict that groups with poorest dispersal ability will experience the highest taxonomic and phylogenetic turnover but a nesting of functional diversity independent of dispersal.

Location: Africa.

Taxa: Rodents, bats, shrews.

Methods: We amassed a continent-spanning dataset of 97 bat assemblages, 166 rodent assemblages, and 153 shrew assemblages comprising a total of 183, 225, and 109 species respectively, from six bioregions of Sub-Saharan Africa. We calculated three aspects of beta diversity: taxonomic, functional, and phylogenetic. For each of these, we first calculated total beta diversity based on the Sørensen index (β_{sor}) and then decomposed this into turnover (β_{sim}) and nestedness (β_{nes}) components. We then used Moran's Eigenvector Maps to examine the relationships between each aspect of beta diversity and environmental gradients (environmental filtering) and geographical distance between sites (spatial processes).

Results: We found consistent patterns across the three taxa in all aspects of beta diversity, with taxonomic beta diversity being greatest and phylogenetic beta diversity being lowest. The turnover component was typically greater than the nestedness component for taxonomic and functional beta diversity, but not for phylogenetic beta diversity, for all three groups. Beta diversity was also linked with the dispersal ability of the three groups, with the highest levels of beta diversity found in shrews, intermediate levels in rodents, and the lowest levels in bats.

Main conclusions: Spatial processes, which are linked to the dispersal abilities of the three taxa of small mammal, dominate environmental drivers in structuring African small-mammal communities with phylogenetic comparisons suggesting a relatively permeable continent.

KEYWORDS

Chiroptera, Rodentia, Eulipotyphla, environmental filtering, spatial processes, turnover, nestedness

1. INTRODUCTION

The processes producing biodiversity patterns, particularly at large spatial scales such as across continents, remain poorly understood (Herkt *et al.*, 2016; Keil & Chase, 2019). Spatial patterns in species richness can best be understood by viewing diversity at different scales, often using three inter-related metrics: alpha, beta, and gamma diversity (Whittaker, 1960; Gardener, 2014; Bennett & Gilbert, 2016) (Figure 1). Alpha and gamma diversities refer to the number of species at a single locality or across a region, respectively, while beta diversity refers to the change in species composition between localities (Baselga, 2010). Hence, beta diversity metrics focus on the variation of diversity, making them particularly useful for understanding patterns of species richness across large macroecological scales (Lennon *et al.*, 2001; Mcknight *et al.*, 2007; Anderson *et al.*, 2011; Varzinczak *et al.*, 2018).

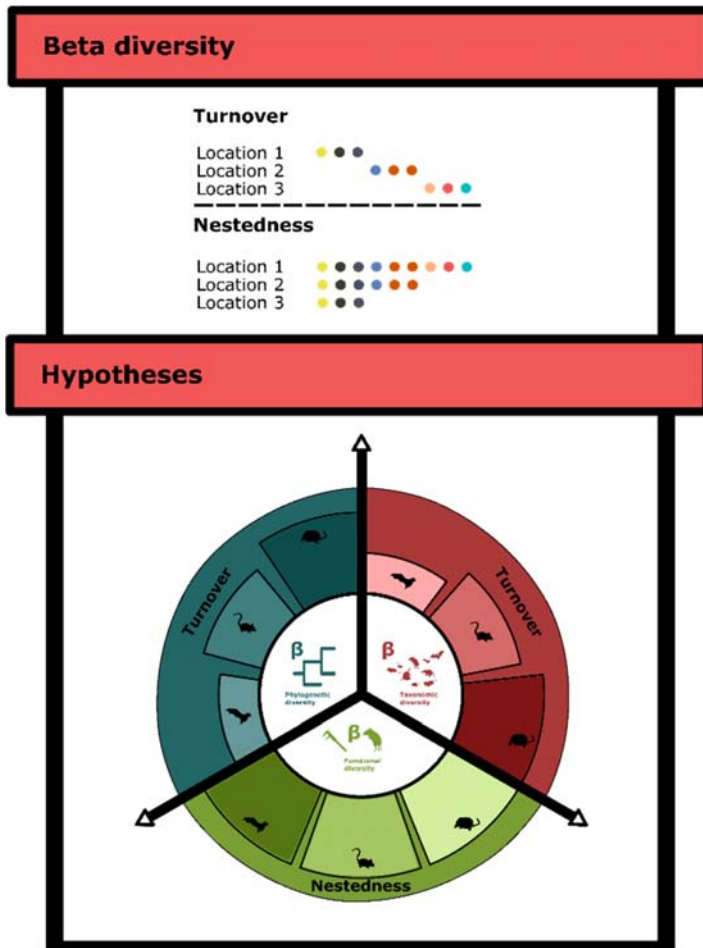


Figure 1. Beta diversity as illustrated by two idealized versions of this metric's subcomponents namely turnover (β_{sim}) and nestedness (β_{nes}). Each coloured spot represents a species. Our **Hypotheses** are split into predicted outcomes for taxonomic, functional, and phylogenetic beta diversity. The height of the segments represents beta diversity. Thus, we predict both phylogenetic and taxonomic turnover to be highest among shrews, intermediate for rodents and smallest for bats. Whereas we predict that functional diversity will be similarly nested across the three taxonomic groups. Silhouettes for the animals in the bottom panel are taken from <http://phylopic.org/>

Three main hypotheses have been put forward to explain patterns of beta diversity across broad continental scales (Varzinczak *et al.*, 2018). First, environmental or niche-based processes may determine the ecological conditions suitable for a species to persist at a particular site (Leibold & Mikkelsen, 2002). Second, spatial processes may differentially affect the ability of species to disperse and hence to occupy geographically distant regions (Leibold *et al.*, 2004). Finally, historical or biogeographical processes such as glaciation events may have influenced species distributions, which still bear the legacy of those events (Couvreur *et al.*, 2021). These three hypotheses are not necessarily mutually exclusive but identifying their relative contributions to species distribution patterns may provide useful evolutionary and macroecological insights (Batista *et al.*, 2020). In particular, by decomposing beta

diversity into components that reflect different processes, the drivers of biodiversity can become clearer (Baselga, 2010; Castro-Insua *et al.*, 2016; García-Girón *et al.*, 2019).

Total beta diversity (β_{sor}), can be partitioned into two main components: turnover (β_{sim}), which is a measure of the replacement of species along a gradient; and nestedness (β_{nes}), which reflects the loss of species leading to species poor sites being a nested subset of species rich sites (Baselga & Orme, 2012). This partitioning of beta diversity is important because turnover (β_{sim}) and nestedness (β_{nes}) can be caused by different processes and may show contrasting spatial patterns (Baselga, 2010; Castro-Insua *et al.*, 2016). For example, turnover (β_{sim}) declines while nestedness (β_{nes}) increases with latitude, presumably due to harsher environmental conditions near the poles (Qian & Xiao, 2012; Soininen *et al.*, 2018). In a contrasting example, there is a strong longitudinal effect in species turnover (β_{sim}) of South American rodents, as a result of the elevational gradient created by Andes (Maestri & Patterson, 2016). Turnover (β_{sim}) and nestedness (β_{nes}) may also be affected by species traits; species that are good dispersers are expected to have lower turnover due to their ability to move across the landscape (Qian & Ricklefs, 2012; Soininen *et al.*, 2018).

The diversity of biological communities has most commonly been studied in terms of species (or taxonomic) richness, which deals with species entities (Melo *et al.*, 2009; Maestri & Patterson, 2016). However, the diversity of a community can also be measured in terms of other aspects such as phylogenetic and functional diversity (Mcknight *et al.*, 2007; Penone *et al.*, 2016; García-Navas, 2019) (Figure 1). Phylogenetic richness takes into account the evolutionary relationships between species and is commonly calculated as the total branch lengths of a phylogenetic tree that connect the group of species in question (Chao *et al.*, 2014; Varzinczak *et al.*, 2018). In contrast, functional richness can be viewed in terms of how species in a community vary in terms of traits that may include morphological features (Villéger *et al.*, 2013; Bishop *et al.*, 2015). Indeed, functional traits can be used to identify factors influencing dispersal ability across taxa such as flight capacity, metabolism, and body mass (Qian & Ricklefs, 2012).

These three measures are closely related and therefore are expected to show similar broad trends; however, it is where their trends deviate or become “decoupled” that they become most informative (Penone *et al.*, 2016; Du *et al.*, 2021). In particular, functional beta diversity is expected to be low across sites with similar environments due to

convergent evolution selecting similar morphological adaptations at these sites (Villéger *et al.*, 2013; García-Navas, 2019). In contrast, phylogenetic beta diversity is expected to be lowest across sites that are linked within a continuous region without severe geographical barriers (Penone *et al.*, 2016). Hence, regions with similar environments but separated by biogeographical barriers are expected to have low functional beta diversity but high phylogenetic beta diversity and vice versa.

Africa is ideal for testing macroecological hypotheses. Sub-Saharan Africa (Afrotropical region) has a diverse mammalian community that includes over 1570 species (ca. 24% of global mammal richness), marginally second only to the Neotropics (Burgin *et al.*, 2018). The three mammalian orders with the greatest number of species in Africa are the rodents (Rodentia), bats (Chiroptera), and shrews and allies (Eulipotyphla) (Kingdon *et al.*, 2013). These small mammals are also abundant, occurring at high densities and play critical roles in ecosystem functioning (Kunz *et al.*, 2011; Russo & Jones, 2015; Lacher *et al.*, 2016; Fischer *et al.*, 2018; Tschumi *et al.*, 2018). Furthermore, Africa is a vast continent with large environmental gradients and clearly defined bioregions (Brooks *et al.*, 2001; de Klerk *et al.*, 2002; Linder *et al.*, 2012).

Of the three small mammal groups, African species richness has only been mapped for bats (Herkt *et al.*, 2016; Monadjem *et al.*, 2018), which shows peaks in the equatorial zone, particularly at the transition between the rainforest and savanna biomes (Fahr & Kalko, 2011), and tropical uplands (Monadjem *et al.*, 2016). The distribution of African species richness is not known for rodents and shrews, but is thought to peak in the rainforest zone (Happold, 1996). In contrast to patterns of species richness, studies of the patterns of beta diversity are almost entirely lacking for African small mammals. When viewed on a global scale, the phylogenetic beta diversity for African rodents and bats appears to be highest in the Sahel region (immediately south of the Sahara desert in the north of the continent), with an uneven distribution across the rest of the continent (Peixoto *et al.*, 2017). On an African continental scale, phylogenetic beta diversity of muroid rodents between bioregions is high with turnover more important than nestedness; in contrast, the relative contributions of turnover and nestedness were similar for functional beta diversity (García-Navas, 2019).

In this study we compare three measures or aspects of beta diversity (taxonomic, functional, and phylogenetic) each with three components, total (β_{sor}), turnover (β_{sim}), and nestedness (β_{nes}) in these three groups of small mammals

across sub-Saharan Africa (Figure 1). Specifically, we ask whether either environmental (bioclimatic variables) or spatial (i.e. distance between sites) factors had the greater influence on beta diversity metrics. We hypothesized that bats, due to their ability to fly, would be better dispersers across the landscape, which would translate into lower turnover rates and hence lower beta diversity (Varzinczak *et al.*, 2019). In contrast, we expected that rodents and shrews would be inferior dispersers compared to bats, and therefore would demonstrate higher rates of turnover. Our specific predictions for each aspect and component of beta diversity compared across the three taxa are presented in Table 1. We made a further prediction that shrews, due to their generally smaller body sizes and high metabolic rates (Gliwicz & Taylor, 2002) that would limit their dispersal ability, would have higher turnover rates than rodents. Finally, we ask whether the patterns of taxonomic, phylogenetic, and functional beta diversity differ across the region and whether these can be linked to specific bioregions (Linder *et al.*, 2012). Therefore, we predict that shrews would show the highest, and bats the lowest, taxonomic beta diversity between *and* within these six bioregions. Similarly, we predict higher phylogenetic beta diversity in shrews and rodents compared with bats between the bioregions. However, with respect to functional beta diversity, we expect higher nestedness in all three taxa compared with taxonomic beta diversity.

Table 1. Summary of the predictions pertaining to three dimensions of beta diversity (taxonomic, phylogenetic, and functional), each decomposed into turnover (β_{sim}) and nestedness (β_{nes}) as comparing three groups of small mammals: bats, rodents, and shrews.

Aspect	Component	Predictions (continental & within regions)	Predictions (between regions)	Environment vs distance
Taxonomic	β_{sor}	shrews > rodents > bats	shrews > rodents > bats	Shrews and rodents influenced more by
Taxonomic	β_{sim}	shrews > rodents > bats	shrews > rodents > bats	distance; bats (due to ability to fly) more
Taxonomic	β_{nes}	bats > rodents > shrews	bats > rodents > shrews	influenced by environment

Phylogenetic	β_{sor}	shrews > rodents > bats	Greater differences for Southern and Ethiopian regions compared with other pair-wise comparisons	
Phylogenetic	β_{sim}	shrews > rodents > bats	Greater differences for Southern and Ethiopian regions compared with other pair-wise comparisons	
Phylogenetic	β_{nes}	shrews > rodents > bats	Greater differences for Southern and Ethiopian regions compared with other pair-wise comparisons	Bats (due to ability to fly across larger distances) will be phylogenetically more representative at distance sites than rodents and shrews (which are less able to disperse)
Functional	β_{sor}	rodents > shrews > bats	rodents > shrews > bats	Bats (due to ability to cross barriers by flying)
Functional	β_{sim}	rodents > shrews > bats	rodents > shrews > bats	will be functionally more representative at
Functional	β_{nes}	bats > shrews > rodents	bats > shrews > rodents	environmentally similar sites than rodents and shrews (which are less able to disperse across barriers)

2. METHODS

2.1 Species assemblages and biogeographic regions

We obtained information on species assemblages of bats (Chiroptera), rodents (Rodentia), and shrews (Soricidae and Macroscelidae) from the literature (see datafiles on GitHub and Appendix 1 for the sources of this information). We included all bats (11 families in the order Chiroptera), and all shrews (Soricidae), all sengis or elephant-shrews (Macroscelidae), and rodents in the families: Muridae, Nesomyidae and Gliridae.

Although the shrews as defined here (i.e. Soricidae and Macroscelidae) are not monophyletic (c.f. Chiroptera and Rodentia) (Happold & Happold, 2013) we retained this group based on shared morpho-functional characteristics (see below). Similarly, our Chiroptera and Rodentia groups, although based on monophyletic clades are not monophyletic groups *per se* since they do not include all the species of the group but only the assemblage of species observed in our study group based on their common morpho-functional characteristics. Therefore, throughout the manuscript, we will refer to bats, rodents, or shrews as the observed morpho-functional groups rather than the cladistic groups. Note that this is taken into account through the phylogenetic analyses described below. Members of the Muridae (murine rodents) and Nesomyidae (African pouched mice) are closely related, in the superfamily Muroidea (Happold, 2013). To this we have added a distantly related family, the Gliridae (dormice), due to their ecological similarity to some arboreal members of the Muroidea (Happold, 2013; Monadjem *et al.*, 2015). We excluded members of the murid genus *Cricetomys* on account of their enormous size (typically ca. 1 kg or heavier) compared with other species included in this study.

For each group, we defined an assemblage as the collection of species that occurred together at a specific site, based on the results of a published study (see below). We included 97 assemblages of bats, 166 assemblages of rodents, and 153 assemblages of shrews comprising a total of 183, 225, and 109 species, respectively. Species accumulation curves for all three groups have started to taper off (see Figure S7 and Appendix 2 in the Supplementary Information), suggesting that broadly speaking, the dataset can be considered representative of species richness of these three groups in Africa. Species sizes were in the same order of magnitude for the three groups with masses of rodents ranging 3–165 g, shrews 2–200 g, and bats 3–310 g.

Our conditions of including a study depended on meeting the following criteria: 1) the study should have covered both seasons, or should have been an intensively focus survey of at least 14 days; 2) should have used appropriate techniques such as live traps for rodents, mist nets and harp traps for bats, and bucket pitfall traps for shrews; 3) published between 1980 and 2020 inclusive; 4) published in a peer-reviewed journal, book, or report available online; 5) covering an area with capture locations a maximum of 10 km apart for rodents and shrews, and 20 km apart for bats; 6) the study reported on the entire assemblage and not just part of it (e.g. fruit bats, or nesomyid rodents, etc). Most of the chosen studies met all these criteria, however, we included a small number of studies that did not, because they reported communities in poorly represented regions. When conditions were not met, it was mostly due to the study having been published before 1980.

We used the biogeographic regions of Linder et al. (2012), who proposed seven regions: Saharan, Sudanian, Congolian, Ethiopian, Somalian, Zambezan, and Southern (Figure 2). Since our focus is sub-Saharan Africa, we excluded the Saharan region from our analysis. We assigned each of the site-specific assemblages for the three groups, bats, rodents, and shrews (see above) to one of these six bioregions (Figure 3).

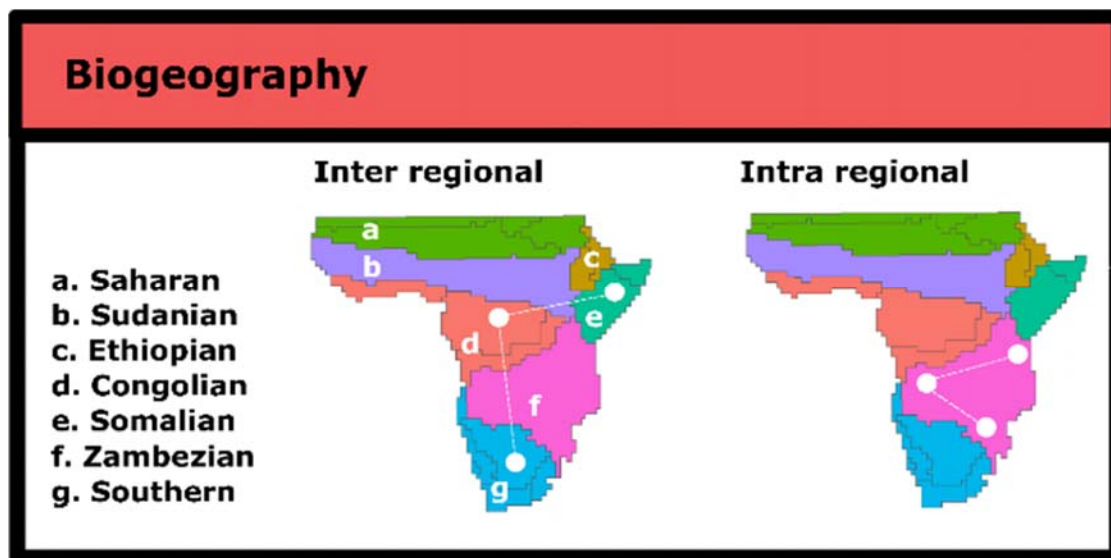


Figure 2. Maps showing seven African bioregions (based on Linder et al. 2012), six of which were compared in our study – the Saharan region is not used in this study. We draw a distinction between the intra and inter regional comparisons for African small mammals (bats, rodents, shrews).

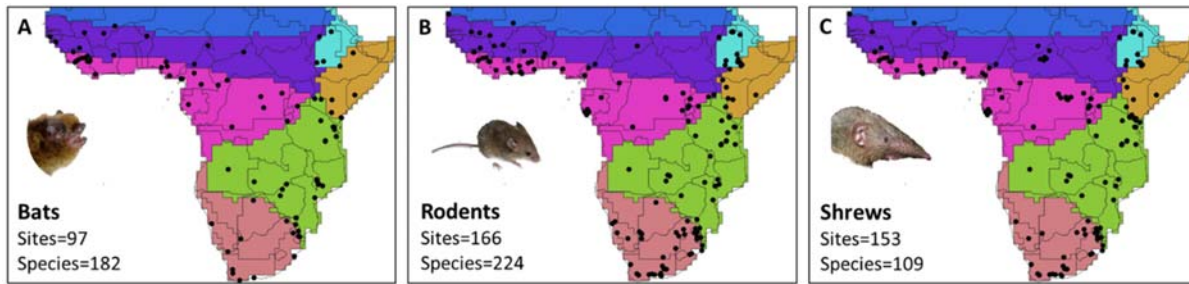


Figure 3. Maps of the study sites (black circles) included in this study for bats (A), rodents (B), and shrews (C). The bioregions are shown in different coloured backgrounds, from north-west to south: dark blue – Saharan; violet – Sudanian; pink – Congolian; light blue – Ethiopian; yellow-brown – Somalian; green – Zambezan; brick – Southern.

2.2 Measuring the aspects and components of beta diversity

We calculated three aspects of beta diversity: taxonomic, functional, and phylogenetic. For each of these, we first calculated total beta diversity based on the Sørensen index (β_{sor}) and then separated this into turnover (β_{sim}) and nestedness (β_{nes}) components using the R package ‘betapart’ (Baselga *et al.*, 2018). We then calculated beta diversity within and across the six bioregions representing the intra and inter biogeographic community comparisons (Figure 2), as explained in detail below.

Taxonomic beta diversity was based on the variation in species composition of the assemblages of bats, rodents, and shrews. First, we calculated beta diversity for each taxon using the function `beta.pair()` in the package ‘betapart’, which calculates three dissimilarity matrices, namely β_{sor} , β_{sim} , and β_{nes} . This allowed us to compare aspects and components of beta diversity for bats, rodents, and shrews at a continental scale. Second, we reran this analysis within each of the six bioregions (i.e. we compared a site within one bioregion with another site in the same bioregion). To obtain these intra- regional comparisons involved the filtering out of pairwise dissimilarity between sites for those sites that fell within the same bioregion, which was done in R. This analysis allowed us to compare the amount of compositional change within bioregions. Third, we calculated beta diversity between bioregions (taking a site in one bioregion and comparing it with a site in another bioregion), again using the function `beta.pair()`. To obtain these inter-regional comparisons we filtered out sites that fell in different regions. This analysis allowed us to determine gross compositional differences between the six bioregions.

We based functional beta diversity on variation in morphological and locomotory traits of the species in the assemblages. These traits included mass, and several external and cranial measurements for each species (see Table S3 for a full list of the traits used). Information on these traits was obtained from published works (Happold 2013; Happold & Happold 2013; Monadjem et al. 2015, 2020). Functional beta diversity was calculated using the function `functional.beta.pair()` from the package 'betapart' (Baselga et al. 2018). A requirement of this function is that the number of species per site must be higher than the number of traits used in the analysis (Baselga et al. 2018). As a result, Principal Component Analysis (PCA) was used to reduce the number of traits, with the first three axes being used in the functional beta diversity analysis. The accumulated proportion of variance explained by these first three axes for bats, rodents and shrews was 95.1%, 93.6% and 95.8%, respectively. This meant that sites needed to have at least four species in order to be included in this analysis. This was not a problem for the bat and rodent assemblages. This was a problem, however, for the shrew assemblages, where a large number of sites would have had to be excluded from the analysis. To reduce the number of sites lost, we included just two axes from the PCA analysis for shrews. This still resulted in the exclusion of 67 (44%) sites with just one or two species. The calculation of functional beta diversity in 'betapart' was then conducted as for taxonomic beta diversity described above.

We calculated phylogenetic beta diversity following the same logic as the taxonomic beta diversity but by taking each species' evolutionary history into account. We scaled the beta diversity using the branch lengths expressed in time since last common ancestor (millions of years ago; Mya) using the chronogram from Upham et al. (2019) and calculated the phylogenetic beta diversity using `phylo.beta.pair()` (Baselga et al. 2018). This analysis allowed us to determine the compositional differences between the six bioregions similarly to the taxonomic diversity part (see above) but using an approach based on Faith's phylogenetic diversity (Faith et al. 2009) to take into account the evolutionarily disparity of each set of communities (Baselga et al. 2018).

We tested the difference between beta diversity values of bats, rodents and shrews for each aspect (taxonomic, functional, phylogenetic) and component (β_{sor} , β_{sim} , β_{nes}) of beta diversity using the Kruskal-Wallis rank test (Chan & Walmsley, 1997).

2.3 Testing influence of environment and spatial processes on beta diversity

We obtained the three dissimilarity matrices β_{sor} , β_{sim} , and β_{nes} as explained above. We then used principal coordinate analysis (PCO) with the function `dudi.pco` from the package `'ade4'` (Dray *et al.*, 2022), with an output of a matrix of orthogonal PCO eigenvectors for each of taxonomic, trait and phylogenetic dissimilarity patterns. We chose the first 10 axes to beta diversity patterns in subsequent analyses.

For our environmental variables, we used the 19 BIOCLIM variables and elevation from the WorldClim database (Hijmans *et al.*, 2005) and elevational roughness to extract bioclimatic variables for each of our sites for assemblages of bats, rodents, and shrews (see Table S1 for definitions of the 19 BIOCLIM variables). To deal with multicollinearity between these variables, we used Variance Inflation Factor (VIF) to select a set of uncorrelated environmental variables. We did the selection process manually, by calculating the VIF for all 21 variables and removing the variable with the highest VIF, and then repeating the process until we were left with seven variables: elevation, elevational roughness, BIO2, BIO3, BIO15, BIO18, and BIO19 (see Table S1 for definitions). The VIF values for these seven variables ranged from 1.39 to 2.18, showing no multicollinearity. These seven variables then formed our environmental variables for subsequent analyses. Because the data we used in this study were collected over the relatively recent past (since 1980), the climatic variables from BIOCLIM should still possess explanatory power over the distribution of the communities of small mammals.

We used Moran's eigenvector mapping (MEM) to analyse spatial variation and structure in beta diversity of small mammals and any association of these patterns with our environmental variables (Borcard & Legendre, 2002; Dray *et al.*, 2006; Benone *et al.*, 2020). The first step was to create the spatial weighting matrix (SWM) which is a network representation of our study sites, with sites as nodes and connections between them as edges. We tested four configurations - Delaunay triangulation, Gabriel, relative neighborhood, and minimum spanning tree (Legendre & Legendre, 2012; Borcard *et al.*, 2018). We chose from among these four methods, the SWM with the highest value of AdjR2. We then used the best SWM to calculate the statistically significant spatial eigenvalues (MEMs) using the function `listw.select()` from the package `'adespatial'` (Dray *et al.*, 2021).

Finally, we used variation partitioning to calculate the contribution from environmental variables and spatial processes in explaining the patterns of the three components of beta diversity for bats, rodents and shrews (Borcard

et al., 2018). Variance partitioning calculates the variation explained by space (distance) alone, the variation explained by environmental variables alone, and then the variation explained by both distance and environmental variables combined, as well the fraction of unexplained variation, called the residual (Borcard *et al.*, 2018). The use of MEMs and variance partitioning to separate the fraction of variation explained by environmental variables versus spatial distance is fully explained Borcard *et al.* (2018) and has recently been performed by other researchers (Widenfalk *et al.*, 2016; Hansen *et al.*, 2020).

All statistical analyses were conducted in R v3.3.6 (R Core Team, 2019). For further details on our analyses, see our code and data at: https://github.com/kanead/beta_diversity.

3. RESULTS

3.1 Beta diversity across the continent

For all three groups, total beta diversity (β_{sor}) was highest for the taxonomic aspect, intermediate for the functional aspect, and lowest for the phylogenetic aspect (Figure 4). Turnover (β_{sim}) accounted for most of the decomposed taxonomic beta diversity for all three groups with nestedness (β_{nes}) contributing little for the majority of comparisons between sites (Figure 4), indicating that the species composition of bats, rodents, and shrews change mostly by replacement rather than sub-setting. Taxonomic beta diversity (β_{sor} as well as β_{sim}) was highest in shrews, intermediate in rodents and lowest in bats, indicating that the species composition of shrew communities was more different between localities compared with rodents and bats (see Table S2 for test statistic results). There was high variability in decomposed components of functional beta diversity, with rodents showing relatively high turnover (β_{sim}) and low nestedness (β_{nes}), in contrast to bats and shrews that had similar values for these two components (Figure 4). Phylogenetic beta diversity was relatively low for all comparisons, with the relative contribution of nestedness higher than for taxonomic beta diversity, but lower than for functional beta diversity.

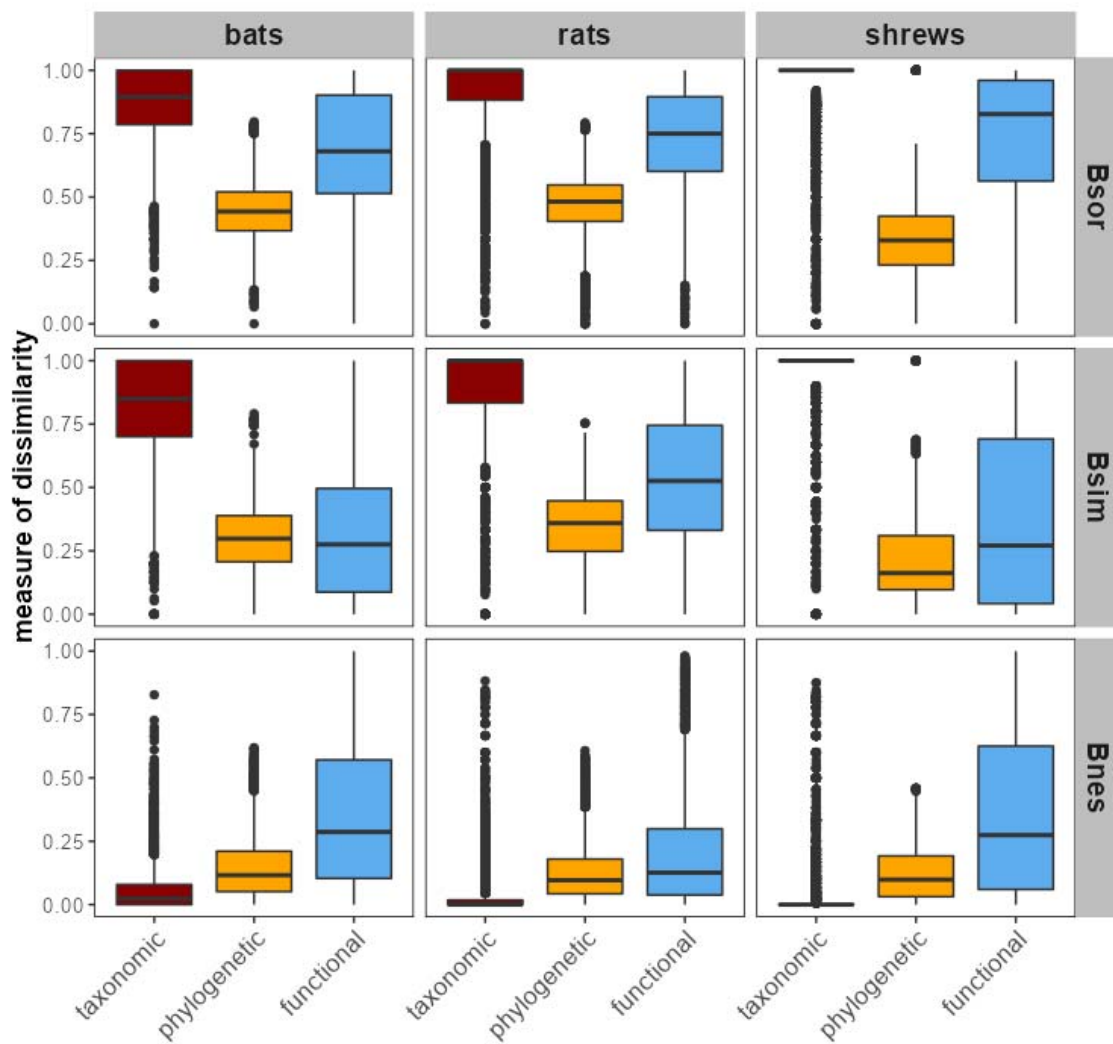


Figure 4. Dissimilarity metrics for three aspects (taxonomic, functional, and phylogenetic) and three components (total: β_{sor} ; turnover: β_{sim} ; and nestedness: β_{nes}) of beta diversity for bats, rodents, and shrews as measured from site-by-site comparisons in Africa.

3.2 Beta diversity within bioregions

Beta diversity within bioregions generally showed the same basic patterns as seen on a continental scale, with some variation between regions for certain components. Total within-region taxonomic beta diversity (β_{sor}) was lowest in bats, intermediate in rodents, and highest in shrews with the patterning holding across all six regions (Figure S1). A similar pattern was exhibited by turnover (β_{sim}), but the opposite trend was seen for nestedness (β_{nes}) where bats had the highest values and shrews the lowest. In contrast, pairwise comparisons of assemblages within each of the six biogeographic regions were similar for each of β_{sor} , β_{sim} , and β_{nes} , with the exception of rodents in the

Somalian region and shrews in the Congolian regions that showed lower β_{sor} and β_{sim} than in other bioregions (Figure S1).

Patterns of functional beta diversity within regions were more variable than for taxonomic beta diversity especially for shrews and showed contrasting trends for β_{sor} , β_{sim} , and β_{nes} (Figure S2). Total functional beta diversity (β_{sor}) was highest in rodents, intermediate in bats and highly variable in shrews. The turnover component (β_{sim}) accounted for most of the variation in rodents, but for most regions nestedness was higher than turnover in bats (Figure S2). This was particularly the case for the Southern bioregion, suggesting that the shrew communities here were subsets of each other with respect to morphological traits, rather than replacement of traits. Because of the large variation in functional beta diversity present in shrews, generalizations are difficult. However, for both the Zambezian and Southern regions, turnover was far higher than nestedness, suggesting that shrew communities in these two regions were replacing morphological traits as was the case in rodents but not bats.

By contrast, within region comparisons of phylogenetic beta diversity showed highest values of β_{sor} (total) in bats and rodents, and lowest in shrews (Figure S3). However, there was clear variation in within region values for shrews. Notably, the variation of β_{sor} was much greater in the Somalian region for shrews than for any other region or compared with any of the other two groups. In general, values of β_{sim} (turnover) were higher than β_{nes} (nestedness) for rodents, but not for bats and shrews, where these two values were similar (Figure S3). Furthermore, turnover was higher for rodents than for bats or shrews, but nestedness values were similar (Figure S3). Phylogenetic β_{sor} and β_{sim} was higher in the Southern region for shrews compared with other regions, but not for bats or rodents.

3.3 Beta diversity between bioregions

Comparisons of taxonomic beta diversity between regions (i.e., comparing a site in one bioregion with a site in a different bioregion) revealed broadly similar trends for the three small mammal groups although the details differed somewhat. For all three taxa, total beta diversity (β_{sor}) was high, and this was due to high values of turnover (β_{sim}), with low values of nestedness (β_{nes}) (Figure S4). However, for bats, β_{sor} values were typically not as uniformly high for all pair-wise comparisons as for rodents and shrews (Figure S4). Particularly, β_{sor} and β_{sim} values were low for the comparison between the Congolian and Sudanian bioregions, as well as for the Zambezian bioregion and the

Somalian and Southern bioregions. For rodents, in contrast, β_{sor} and β_{sim} values were more uniformly higher than for bats, with slightly lower values for the comparisons between the Sudanian bioregion and the Congolian and Somalian bioregions on the one hand, and the Zambezian bioregion and the Somalian and Southern bioregions on the other hand. For shrews, all β_{sor} comparisons were also high with slightly lower values between the Congolian and Sudanian bioregions and the Zambezian and Somalian bioregions, and turnover values were particularly high for the Ethiopian bioregion compared with the other bioregions (Figure S4).

In contrast to taxonomic beta diversity, functional beta diversity between the regions was low for all three taxa. Functional total β_{sor} was relatively low, except for comparison of the Ethiopian bioregion with the rest of the bioregions (Figure S5). Furthermore, the β_{sor} values were accounted for equally by turnover (β_{sim}) and nestedness (β_{nes}). Similarly, low values of phylogenetic beta diversity were observed for between region comparisons (Figure S6). For all three taxa, β_{sor} values were relatively high for the Southern region in comparison with other regions.

3.4 Influences of environment and distance on beta diversity

Overall, variation partitioning revealed that environmental and spatial variables explained a significant fraction of the variation present in small mammal communities (Figure 5). The relative importance of environmental variables versus spatial distance varied both among the three components of beta diversity (taxonomic, functional, phylogenetic) and among the three groups (bats, rodents, shrews). Spatial processes explained more of the variation in the taxonomic component of beta diversity than in the other two components for all three groups ranging from 26% in bats (Figure 5a) to 36% and 39% in shrews (Figure 5c) and rodents (Figure 5b), respectively. And spatial processes also explained more variation than environmental variables (alone) for all comparisons (e.g. across all beta diversity components and for the three groups of small mammals). For the taxonomic beta diversity component, environmental variables alone explained 7% in bats, but just 2% and 1% in rodents and shrews, respectively.

The comparison of variance partitioning in the functional and phylogenetic components of beta diversity were similar for bats (Figure 5a) and rodents (Figure 5b), but strikingly different in shrews where space explained 23% of the variation in the phylogenetic component but just 12% in the functional component (Figure 5c).

The variance partitioning also identified substantial amounts of variation common to both spatial and environmental processes ranging from 0.05 to 0.30 (Figure 5). These results can be interpreted as environmental gradients across the study sites.

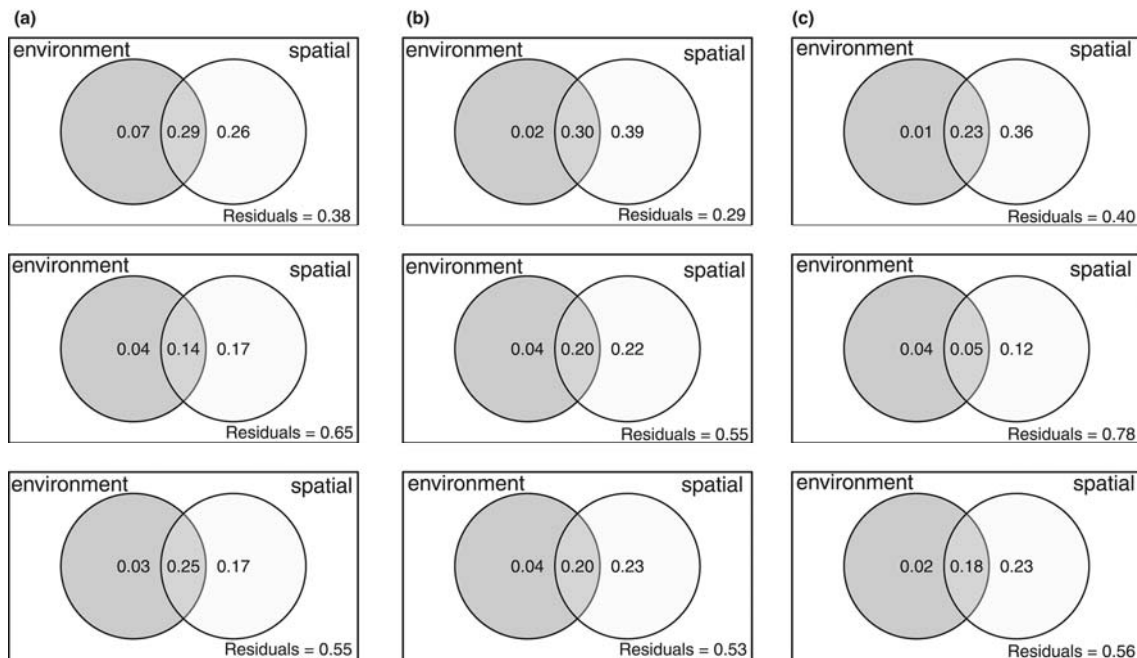


Figure 5. Venn diagrams showing the variance partitioning between environmental and spatial variables for bats (A), rodents (B) and shrews (C) based on Moran’s eigenvector mapping (MEM) analysis of presence data of small mammal communities across the African continent. The top diagram in each of these represents taxonomic beta diversity, the middle diagram functional beta diversity and the bottom diagram phylogenetic beta diversity. The variation explained by environmental variables (‘environment’) alone is presented in the grey shaded circle on the left and that by spatial distance (‘spatial’) alone in the white circle on the right of each diagram. The fraction of variation explained by both environmental and spatial variables is given where the circles intersect. Any remaining unexplained variation is presented as the residuals.

4. DISCUSSION

As we had predicted, taxonomic beta diversity (β_{sor}) was highest in shrews, and lowest in bats, and this pattern held across the continent as well as within individual bioregions. In fact, median β_{sor} and β_{sim} were both 1 for shrews, indicating that there was a complete change in species composition for most pair-wise comparisons between sites. In contrast, β_{nes} was highest in bats, indicating that there was greater nestedness in species composition of bat assemblages than in rodents or shrews. Based on variance partitioning, we were also able to demonstrate that spatial processes accounted for a higher fraction of the explained variation than environmental variables alone and

this fraction was larger for rodents and shrews than for bats. This finding corroborates the results of a recent study of beta diversity patterns in Phyllostomidae bats in the Neotropics (Varzinczak *et al.*, 2018), where they also found that spatial processes better accounted for their results than either environmental filtering or historical dynamics.

With regard to functional beta diversity, our prediction that bats would show lower values of β_{sor} and β_{sim} than either rodents or shrews, was also borne out. The turnover component (β_{sim}) was relatively more important in rodents compared with either bats or shrews, where β_{sim} and β_{nes} were equally important. Hence, African bat and shrew assemblages are composed of species with traits that are a subset of each other. Conversely, rodent assemblages are composed of species with a different set of traits. Why this should be is not obvious, but the difference between functional beta diversity of rodents and shrews may be related to the relatively uniform characteristics of shrews compared with a higher variability in traits present in rodents (Verde Arregoitia *et al.*, 2017). However, bats are at least equally variable with respect to functional traits found in rodents, and the differences in functional beta diversity between these two groups may be related to the greater dispersal ability of bats, allowing the greater influence of environmental filtering (and hence nestedness) of their assemblages (Arita & Rodríguez, 2004).

Finally, regarding phylogenetic beta diversity, our prediction of greater values for bats compared with rodents and shrews was not borne out. Phylogenetic beta diversity values (β_{sor} and β_{sim}) were similar for bats and rodents, and lower only in shrews. Our hypothesis that bats would have lower phylogenetic beta diversity (compared with rodents and shrews) due to their ability to fly, which would therefore act to inhibit speciation by geographic isolation, may have under-estimated the dispersal ability of rodents (Mizerovská *et al.*, 2019). The pattern of taxonomic beta diversity (with higher turnover for rodents compared with bats), demonstrates that individual rodent species change more rapidly across space than bats species. However, this pattern probably breaks down at higher taxonomic levels (say that of genus), which would explain the observed pattern in functional beta diversity. In addition, there are few severe restrictive physical (geographic) barriers within Africa, at least compared with South America where the Andes form a formidable barrier down the entire length of the continent, which has had major influences on beta diversity of the regions rodents (Maestri & Patterson, 2016). By contrast, there are no mountain chains of comparable length and size in Africa, and hence barriers to movement of small mammals are probably less

of a challenge in Africa compared with South America. This would explain the relatively low phylogenetic beta diversity values across all groups observed in this study.

Across all three taxa, beta diversity and turnover values (β_{sor} and β_{sim}) were highest for the taxonomic aspect, intermediate for the functional aspect, and lowest for the phylogenetic aspect. This consistency between taxa suggests similarity in the processes involved. The higher taxonomic beta diversity values are probably due to the high number of species in each of these three groups, with typical species having relatively small geographic ranges (Happold, 2013; Happold & Happold, 2013). Hence, pair-wise comparisons between sites are expected to show high turnover, due to dissimilarity in species composition between them. In contrast, the lower functional beta diversity values of β_{sor} and β_{sim} reflect constraints on the morphology of these species; within all three taxa species are built to generally the same basic body plan e.g. all bats have wings and can fly. This is supported by the observation that the nestedness component of functional beta diversity was typically high. The consistently low phylogenetic beta diversity values of β_{sor} and β_{sim} for the three groups, are probably due to the lack of geographic barriers as discussed in the previous paragraph.

We had predicted that the Southern and Ethiopian bioregions would have higher values of phylogenetic beta diversity, compared with pair-wise comparisons of other bioregions. This was borne out for comparisons involving the Southern bioregion but not the Ethiopian region. Southern Africa has had a long history of relative biogeographic isolation from the rest of Africa (Werger, 1978), which may explain this pattern. Furthermore, in the case of the “shrew” taxon, the southern African region includes multiple species of sengis (order Macroscelidea) in addition to soricid shrews (order Eulipotyphla); but other than East Africa, sengis are generally absent from other bioregions of sub-Saharan Africa (Kingdon *et al.*, 2013). Sites with Macroscelidea can impact phylogenetic diversity results because of the higher variance in branch lengths in these assemblages. Why the Ethiopian region does not also show high values of phylogenetic beta diversity is not readily apparent, especially given the high levels of endemism here (Bryja *et al.*, 2019). Another source of bias may lie in the sites that we selected for inclusion in our analysis, which represent localities that were chosen for surveys of small mammals by previous researchers and may therefore not be representative of the biogeographic regions used in our analyses; a broader sampling of sites within each bioregion may provide additional fruitful insights.

Africa's geological history and climatic fluctuations have undoubtedly had a major influence on diversity patterns past and present (Plana, 2004; Couvreur *et al.*, 2021). Of particular note are the major mountain building events that, when coupled with shifts in the climate resulting in the expansion/contraction of rain forests, would have isolated populations and thus afforded multiple opportunities for speciation through vicariance (Morley, 2000; Loader *et al.*, 2007; Couvreur *et al.*, 2021). The past 11 million years (Myr) has witnessed a surge in African biodiversity in the tropics. Indeed, in their review of the continent's biogeography, Couvreur *et al.* (2021) reported that two thirds of African biota originated in the last 5 Myr, which coincides with the emergence of the extant species including in this study. Hence, we expect that their evolution has been more influenced by relatively recent events rather than during the events that witnessed the major geological changes that took place deeper in the past (e.g. Stadelmann *et al.* 2004; Nesi *et al.* 2013; Taylor *et al.* 2014; Bryja *et al.* 2017; Nicolas *et al.* 2019, 2021). Incorporating historical elements remains a challenge given the coarse-scale (both spatial and temporal) understanding we have of the past climates and habitats of the continent (Couvreur *et al.*, 2021). Nonetheless, future studies would do well to integrate the influence of historical processes on beta diversity patterns of African small mammals.

By integrating all three components of beta diversity in our study, we are able to provide a deeper understanding of the processes affecting the composition of African small mammal communities (Penone *et al.*, 2016). For example, in our study bat communities typically had lower turnovers across Africa than shrews or rodents when the comparison was made by using species (i.e. taxonomic beta diversity). However, turnover in the phylogenetic component of beta diversity showed a different pattern, with shrews having lower turnover compared with bats and rodents, suggesting limited historical isolation in shrews. Turnover in functional beta diversity was again different with rodents having higher turnover compared with bats and shrews, suggesting that rodents exhibit greater variability in morphological features (i.e. more labile) than bats or shrews which are more conservative. Hence, niche conservatism (Wiens *et al.*, 2010) may be more important for bats and shrews than for rodents. If we consider the implications of our findings for the persistence of these groups, bats may be well served by their dispersal ability, rats by their lack of niche conservatism, with shrews less well adapted to global change.

In conclusion, although both environmental filtering and spatial processes have influenced taxonomic beta diversity of the three small mammal groups, spatial processes explained more of the variation than environmental ones.

Decoupling these effects are a common issue in biogeography due to the possibility of spatial structuring of environmental variables (Varzinczak *et al.*, 2018). Hence, further understanding of the mechanisms regarding these processes will require approaches that incorporate further taxonomic groups and other continental scales. For instance, a comparison of bats with bird assemblages would be informative because both are readily able to disperse given their capacity for flight. In line with our predictions, we found consistent spatial structuring of beta diversity in the three taxa. These patterns underscore the importance of dispersal ability in influencing the composition of small mammal assemblages.

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Biosketch

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