Spatial Scale Effects on Elevational Diversity Gradients: Insights from Kenya's Montane Small Mammals

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Additional file 2

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1 Extended Account of the Study Areas

We focused on small mammals in the orders Rodentia, Eulipotyphla, and Macroscelidea across the highest peaks in Kenya—Mount Kenya, Mount Elgon, Aberdare Ranges, Cherangani Hills, Mathews Range, Mount Kulal, and Chyulu Hills (**Error! Reference source not found.**, Additional file 2). They feature unique topographies associated with their origins from tectonic activities and volcanic eruptions between the Miocene and Pleistocene epochs tied to the East

African Rift System (Haug & Strecker, 1995; Delvaux & Khan, 1998; C. Morley *et al.*, 1999; Küper *et al.*, 2004; Chorowicz, 2005; Ebinger, 2005; Wichura *et al.*, 2010; Veldkamp *et al.*, 2012; Furman *et al.*, 2016; Mairal *et al.*, 2017). Mount Kenya, Mt. Elgon, Aberdare Range, Mt. Kulal, and Chyulu Hills formed through volcanic activity, with their structures dominated by volcanic cones and craters, whereas the Cherangani Hills and Mathews Range formed through tectonic processes. The diverse landscapes and microclimates created by their formation led to rich biodiversity and high levels of endemism, with fertile volcanic soils and varied altitudes supporting diverse ecosystems, providing habitats for a wide array of flora and fauna (Korner & Spehn, 2019). They also act as ecological refuges, enabling species to persist and adapt during climatic changes. Their geographical isolation also promotes endemism and species evolution, and the surrounding areas act as barriers, fostering species differentiation (Mamantov *et al.*, 2021; Males *et al.*, 2023). Together, they are critical biodiversity hotspots, serving essential roles in water catchments and ecological balance and supporting wildlife conservation and the livelihoods of local communities (Western *et al.*, 2015). Worryingly, these mountain ecosystems are characterized by a lack of dedicated formal accounts of their biodiversity patterns and driving processes, especially for small mammals, which are nonexistent for most and one or two others, such as Mount Kenya.

Importantly, these mountains not only serve as critical biodiversity hotspots but also play essential roles in water catchment and climate regulation, underpinning both ecological integrity and the livelihoods of local communities (Hedberg, 1969; Haug & Strecker, 1995; Prodehl *et al.*, 1997; Delvaux & Khan, 1998; C. Morley *et al.*, 1999; C. K. Morley *et al.*, 1999; de Klerk *et al.*, 2002; Küper *et al.*, 2004; Chorowicz, 2005; Ebinger, 2005; Burgess *et al.*, 2007; Hopp *et al.*, 2007; Veldkamp *et al.*, 2007; Nicolas *et al.*, 2008; Nonnotte *et al.*, 2008; Taylor *et al.*, 2009;

Wichura *et al.*, 2010; Veldkamp *et al.*, 2012; Bartakova *et al.*, 2013; Engel *et al.*, 2014; Schüler *et al.*, 2014; Demos *et al.*, 2015; Jacquet *et al.*, 2015; Furman *et al.*, 2016; Mairal *et al.*, 2017; Murungi *et al.*, 2017; Bryja *et al.*, 2018; Hughes *et al.*, 2018; Mazoch *et al.*, 2018; Sumbera *et al.*, 2018; Voelker *et al.*, 2021; Dianat *et al.*, 2023).

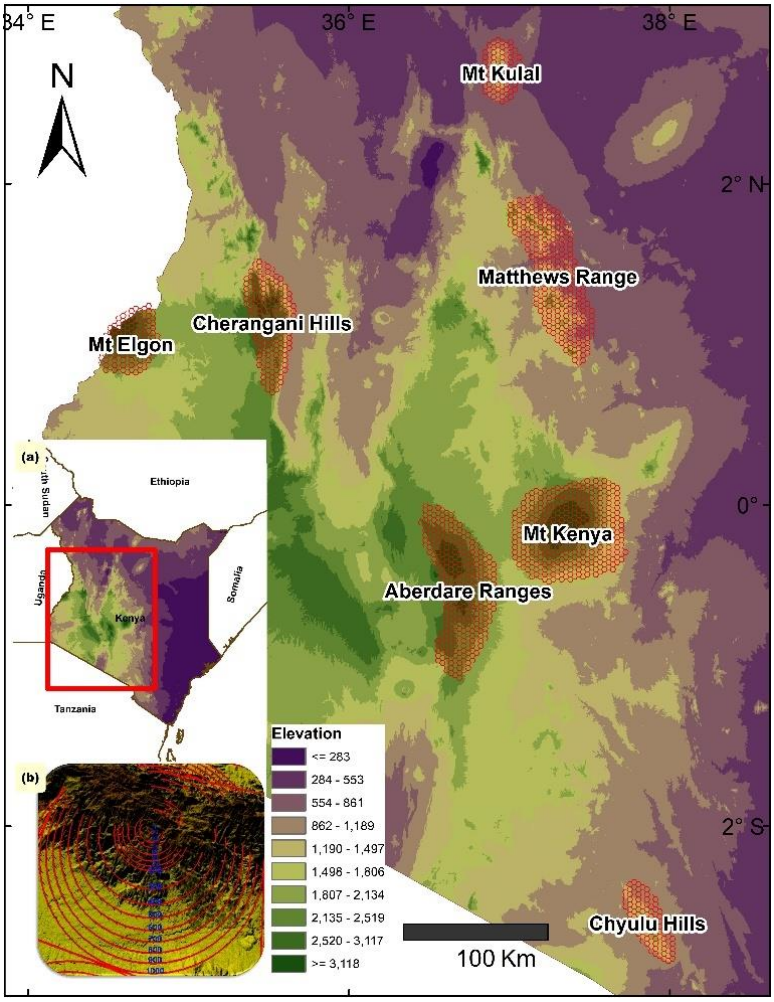

Figure 1. Topographical maps of the study sites and illustrations of the sampling scheme. The figure shows the location and names of the studied mountains in Kenya. The inset figures show the geographical locality of the sampled mountains within Kenya (a) and an illustration of the strictly nested quadrat design used in the study rendered on a digital elevation model map layer (b) – the red lines indicate transect boundaries.

For each mountain, we designed spatially varied sampling windows/grain sizes (Barton *et al.*, 2013) using the strictly nested quadrat method (Leitner & Rosenzweig, 1997), which yields type

I species-area curves in Scheiner (2003). Thus, we maintained the spatial extent and shape of the sampling window while varying the sampling grain/unit, guided by the spatial scale concept's two key aspects: the spatial extent (overall size of the area considered in a specific study) and spatial grain or resolution (the dimensions of the individual spatial units within that area, for which observations or predictions are made). This approach ensures more accurate estimates of expected species richness for a randomly located plot within a given area, allowing for direct associations between species turnover and aggregation patterns across regions (Scheiner, 2003; Barton *et al.*, 2013). We overlaid grids spanning the extents of mountains for each spatial grain size—0.0001, 0.001, 0.01, 0.1, 1, 2, 4, 6, 8, and 10 km^2—resulting in ten community datasets for each mountain. The spatial grain sizes were defined by leveraging our data resolution, previous studies, and the field sampling scale at which small mammal communities demonstrate unique biogeographic diversity (de la Sancha *et al.*, 2020; Onditi *et al.*, 2022). The largest grain size was used as the sampling baseline grain size for the consecutively smaller units. Each subsequent smaller-grain grid was created by determining the centroid of the baseline grid and then creating a buffer of varied radii around it. The radii lengths were back-calculated to match the predetermined grid sizes using the formula *Pi multiplied by the squared radius ($A = \pi r^2$)*. Due to the different geomorphological characteristics of the mountains (lateral extents and peak-base heights), as highlighted in the section above, we ultimately sampled variable numbers of grids per mountain determined based on the transition in environmental conditions (histograms of the climate and elevation data), vegetation, and species turnover from the surrounding lowlands. The variable lateral extents and peak-base heights between mountains resulted in 458 grids at Mount Kenya (spanning 1,090–4,642 m), 134 at Mount Elgon (1,854–4,154 m), 371 at Aberdare

Ranges (1,830–3,816 m), 212 at Cherangani Hills (932–3,416 m), 357 at Mathews Range (651–2,434 m), 99 at Mount Kulal (592–1,899 m), and 112 at Chyulu Hills (967–1,954 m).

1.1. Mount Kenya

Mount Kenya, Africa's second-highest peak at 5,199 meters, is an extinct stratovolcano formed approximately 2.6 and 3.1 million years ago during the Pliocene epoch. Its formation is intrinsically linked to the tectonic activities of the East African Rift System, where the Arabian and African Plates are moving apart. The resulting volcanic activity built up layers of solidified lava and ash, creating the mountain's massive structure, rugged peaks, and glacial valleys (Baker, 1967; Hastenrath & Kruss, 1992; Mahaney *et al.*, 2012; Maslin *et al.*, 2014; Loomis *et al.*, 2017). The mountain's volcanic origins have produced rich, fertile soils that support diverse vegetation zones ranging from montane forests at the base to alpine meadows and moorlands toward the peak. Its distinct elevational gradients and habitat heterogeneity create a variety of microclimates, fostering high levels of endemism and biodiversity, including species adapted to harsh alpine conditions. Mount Kenya is one of the most species-rich areas for small mammals, supporting a wide array of flora and fauna, including local endemics like the Mount Kenya mole-rat. Ecologically, Mount Kenya exhibits a pronounced wet–dry characterization. The southeastern slope, being the windward side, receives approximately 2,500 mm of average annual rainfall. This moisture supports a succession of vegetation types: mixed Afromontane rainforest bordering farmed areas at the base, followed by bamboo forest, undifferentiated forest, and Montane Ericaceous vegetation toward the peak. The northwestern slope—the leeward side—is comparatively drier, receiving about 800 mm of rainfall. It primarily supports Afromontane undifferentiated forests from the base to mid-elevations and Montane Ericaceous vegetation above (Musila *et al.*, 2019; Onditi *et al.*, 2022). Recent surveys have revealed a high

diversity of small mammals on Mount Kenya, with phylogenetic and functional diversity trends contrasting with species richness. The mountain serves as a biodiversity hotspot and a refuge for species affected by climatic changes. Its significance in natural ecology and ecosystem services is recognized through its designation as a UNESCO World Heritage site, an important bird area, and a key biodiversity area. Beyond biodiversity conservation, Mount Kenya provides essential ecosystem services that underpin wildlife preservation and local communities' livelihoods (Bennun & Njoroge, 1999; Brown & Hay-Edie, 2014).

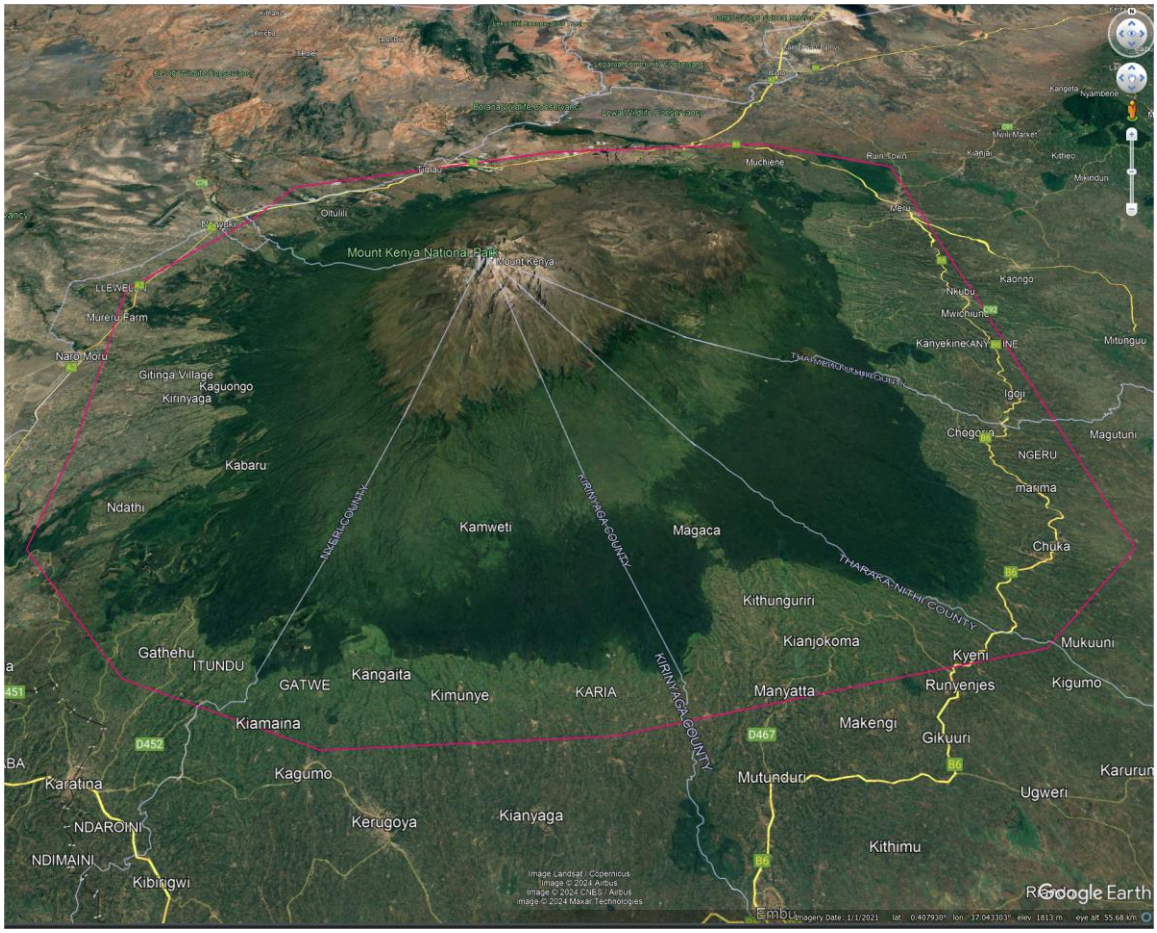

Figure 2. Satellite image of Mount Kenya showing the outline of the study site. The elevation is shown with an exaggerated rendering to aid in visualizing the spatial extent of the mountain.

1.2. Mount Elgon

Mount Elgon, an extinct shield volcano on the Kenya-Uganda border, reaches an elevation of 4,321 meters and is one of East Africa's oldest volcanoes, formed approximately 24 million years ago during the Miocene epoch (Cameron *et al.*, 2000; Nield *et al.*, 2000; Ongugo *et al.*, 2002; Vedeld *et al.*, 2005). Its broad, gentle slopes—characteristic of shield volcanoes formed by low-viscosity lava flows—feature a vast caldera and numerous lava tube caves. Although slightly removed from the central axis of the Great Rift Valley, Mount Elgon's formation is related to regional tectonic stresses and volcanic activities associated with the East African Rift System. The mountain's long geological history has allowed ecosystems to mature and diversify. Unique features like the caldera and lava tube caves provide specialized habitats, supporting rare plant species and endemic animals in the montane forests and Afro-alpine zones. The isolation and varied habitats contribute to high levels of endemism and biodiversity, making Mount Elgon a vital conservation area. The national park covers about 1,279 km² and showcases diverse ecosystems influenced by elevation. Surrounding lands are utilized for agriculture, highlighting the balance between conservation and human use in the region.

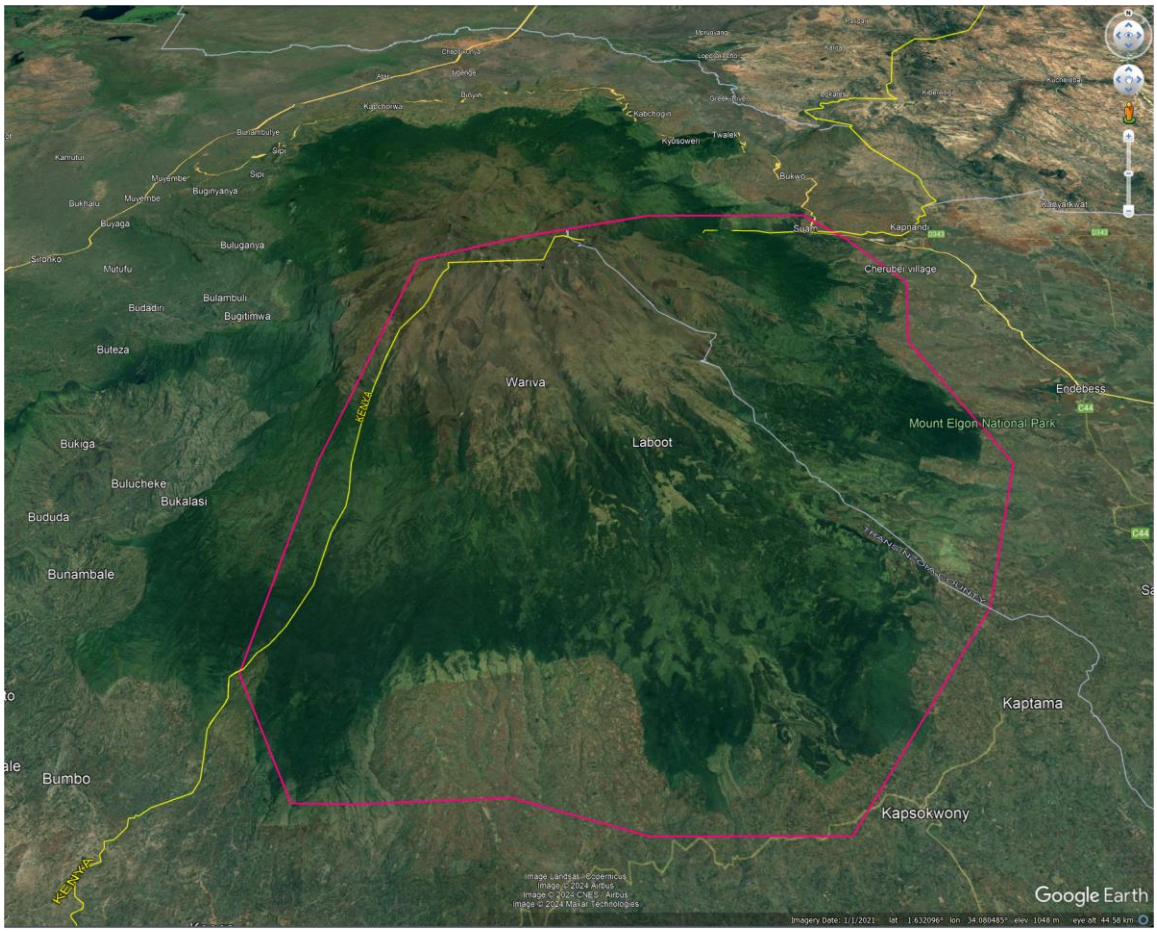

Figure 3. Satellite image of Mount Elgon showing the outline of the study area (red outline). The yellow line is the administrative boundary between Kenya and Uganda.

1.3. Aberdare Range

The Aberdare Range, also known as the Nyandarua Range, is located west of Mount Kenya and stretches over approximately 160 kilometers, with peaks reaching up to 3,999 meters (Hedberg, 1969; Gichuki, 1999; Lambrechts *et al.*, 2003). This highland formation consists of steep forested ravines and open moorlands, representing the eroded remnants of a large shield volcano formed from volcanic activities linked to the East African Rift System during the Pliocene to Pleistocene epochs (about 5.3 million to 11,700 years ago). Situated along the eastern edge of the Great Rift Valley, the range is part of the uplifted regions resulting from tectonic forces

associated with the rifting process. The region's high rainfall sustains lush montane forests and bamboo zones, fostering diverse habitats that support rich biodiversity. The varied altitude and climate create multiple ecosystems—including rainforests, bamboo forests, and moorlands—crucial for water catchment, supplying rivers like the Tana and Athi. The steep western slopes sharply descend into the Kinangop Plateau and the Rift Valley, while the eastern slopes descend more gradually. Like Mount Kenya, the Aberdare Range's diverse habitats support numerous species, emphasizing its importance for conservation and ecological balance in the region.

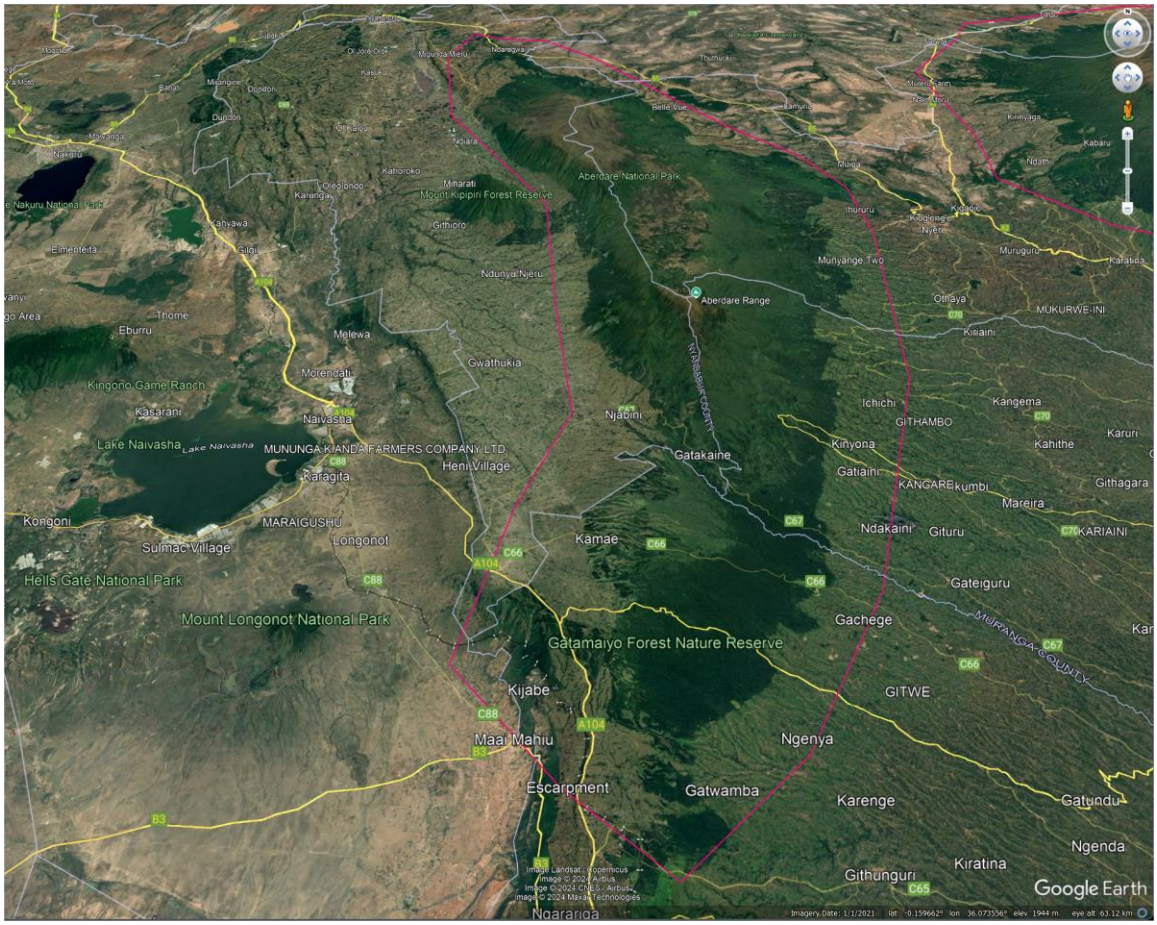

Figure 4. A satellite image of the Aberdare Ranges showing the outline of the study area.

1.4. Cherangani Hills

The Cherangani Hills, located in northwestern Kenya along the western flank of the Gregory Rift, reach elevations up to 3,530 meters and consist of a series of rolling hills, forested ridges, and rocky gorges (Davies, 2006; Neumann & Scott, 2018; Rotich, 2019). Composed predominantly of ancient metamorphic rocks with some volcanic intrusions, they were formed through uplift and faulting associated with the Great Rift Valley during the Miocene epoch (approximately 23 to 5 million years ago). The moderate climate supports extensive indigenous forests that are biodiversity reservoirs, home to rich birdlife and mammals. The ecological integrity of the Cherangani Hills is essential for sustaining regional biodiversity and ecological services, emphasizing the importance of conservation in this area.

Figure 5. Satellite image of Cherangani Hills showing the outline of the study area (red outline).

1.5. Mathews Range

The Mathews Range, also known as the Lenkiyio Hills, is a relatively remote mountain range in northern Kenya that stretches approximately 150 kilometers from north to south, reaching elevations up to 2,688 meters (Foster & Gleadow, 1992). The range formed around 5 million years ago during the late Tertiary period through tectonic uplift and faulting associated with the East African Rift System and consists of steep-sided mountains and valleys, creating a “sky island” with unique ecosystems. The semi-arid climate at lower elevations transitions into denser forests in the highlands, supporting diverse wildlife, including endemic flora and fauna adapted

to arid conditions. The isolation and unique climatic conditions have allowed species to evolve independently, enhancing biodiversity and making the Mathews Range a critical area for conservation and ecological studies. The region is an important conservation area and supports pastoralism among local communities, highlighting the balance between ecological preservation and human livelihoods. Its ecological and cultural significance underscores the importance of ongoing efforts to protect and study this unique environment.

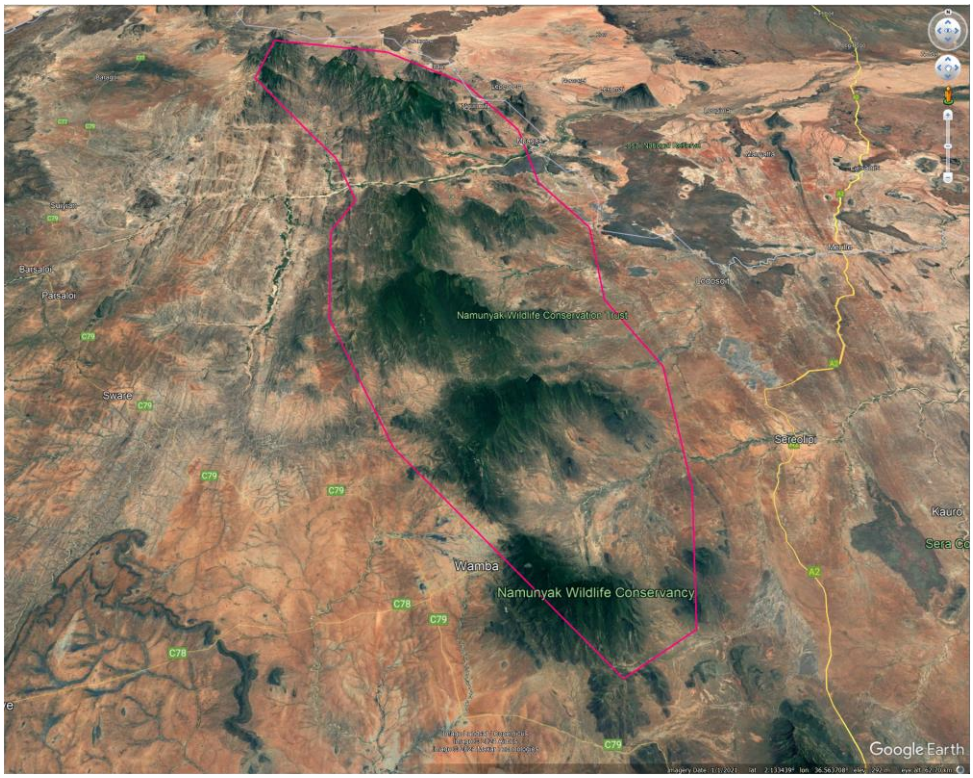

Figure 6. Satellite image of Mathews Range showing the outline of the study area (red outline).

1.6. Mount Kulal

Mount Kulal, an extinct volcano near Lake Turkana in northern Kenya, rises to approximately 2,300 meters and encompasses about 750 square kilometers (Lusigi, 1989; Mäckel *et al.*, 2021). Formed during the Pleistocene epoch through tectonic and volcanic activities associated with the

East African Rift System, it features rugged terrain marked by steep slopes and deep canyons. Mount Kulal creates a unique microclimate in an otherwise arid region, offering a cooler and more humid environment than the surrounding desert. Designated as a UNESCO Man and Biosphere Reserve, Mount Kulal acts as a “sky island,” fostering distinct ecological conditions due to its isolation and elevation. Its montane forests are a haven for diverse bird species and mammals. The mountain is divided into northern and southern sections, with the northern part receiving about 900 to 1,000 millimeters of rainfall annually, compared to 200 to 300 millimeters in the southern part; this variation contributes to its ecological diversity. Mount Kulal’s ecosystems are vital for local biodiversity and serve as an essential ecological corridor.

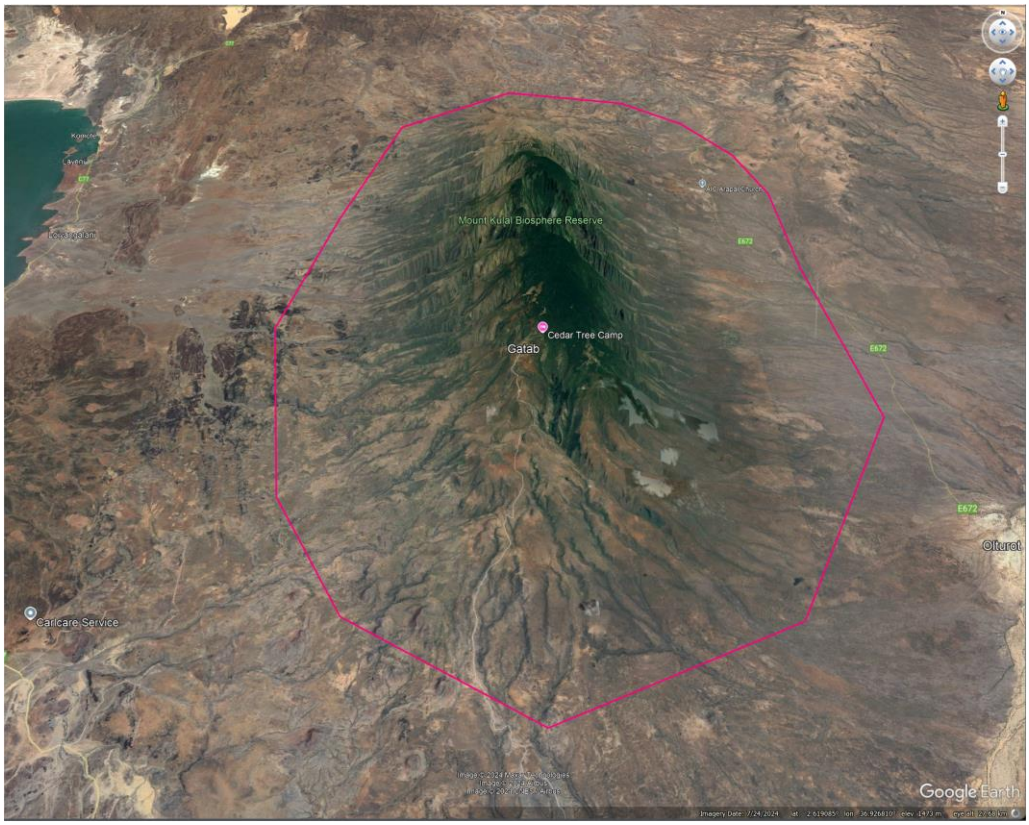

Figure 7. A satellite image of Mount Kulal showing the outline of the study area (red outline).

1.7. Chyulu Hills

The Chyulu Hills are a geologically young volcanic mountain range in Kenya, consisting of numerous volcanic cones and craters. The most recent volcanic activity was recorded in 1856, resulting in fresh lava flows and ash cones. Situated between the Tsavo and Amboseli plains, the hills were formed from volcanic activities related to tectonic movements influenced by the East African Rift System. Formed between 1.4 million years ago and the Holocene epoch (approximately 11,700 years ago), the Chyulu Hills extend over 100 kilometers, and range in elevation from 1,000 meters on the upland plains up to 2,188 meters (Novak *et al.*, 1997a; Novak *et al.*, 1997b). While the surrounding region receives about 400–500 millimeters of average annual rainfall, the peak elevations—covered in evergreen montane cloud forests within grassland–shrub mosaics—receive higher amounts, ranging from 800 to 2,000 millimeters annually (Onditi *et al.*, 2022). The hill provides habitats for numerous bird species and mammals and is crucial for conservation efforts and ecological research. They illustrate the intricate interactions among climate, elevation, and biodiversity, mainly because they are nestled between the expansive Tsavo ecosystems. The recent volcanic soils support unique ecosystems, and the combination of fertile soils and varied climates promotes high biodiversity and endemism.

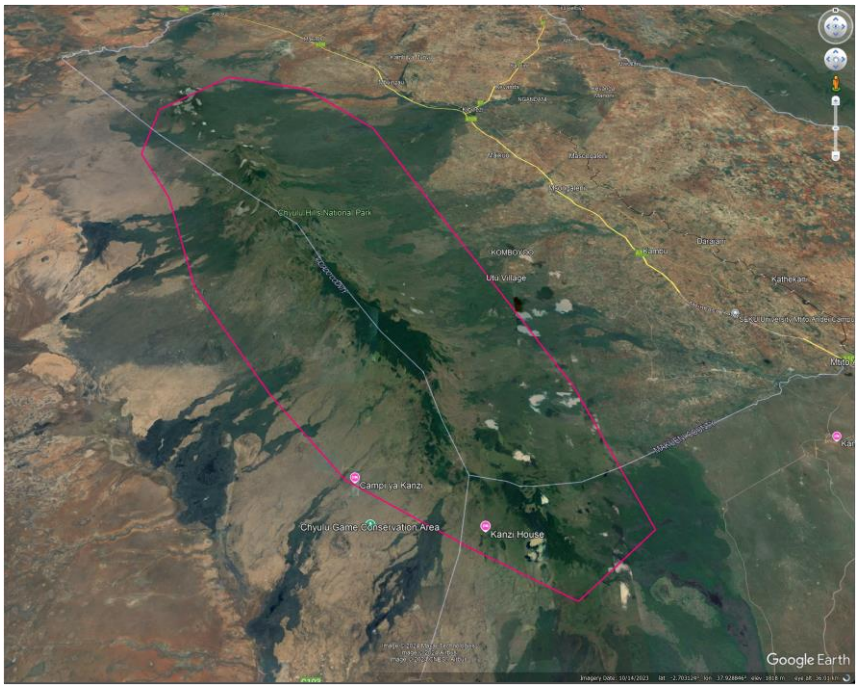

Figure 8. Satellite image of Chyulu Hills showing the outline of the study area (red outline).

2 Extended account of the estimation of diversity indices

We estimated species richness and various phylogenetic and functional diversity indices for a more holistic characterization of the communities. Parameters for diversity indices calculations were carefully chosen based on preliminary analyses and literature review, and the selection of diversity indices was guided by the study's aim to capture both the breadth of evolutionary history and the range of functional traits within montane small mammal communities, providing a comprehensive view of biodiversity (McGill *et al.*, 2006). Following the preliminary explorations, five alpha diversity indices—species richness (SR), phylogenetic diversity (PD), functional diversity (FD), phylogenetic mean nearest taxon distance (PD^{MNTD}), and functional mean nearest taxon distance (FD^{MNTD})—and three multisite beta diversity indices (taxonomic, phylogenetic, and functional) were estimated for each mountain across ten spatial grains. For the estimations, the datasets (species composition matrix, phylogeny, traits, and metadata) were first

curated to ensure that site (grid IDs) and species names exactly matched, using the 'base' and 'picante' R packages with the functions 'match.phylo.comm', 'match.phylo.data', and 'all.equal' (Kembel *et al.*, 2010; R Core Team, 2024).

Species richness (SR) was estimated based on the presence-absence sum of unique species to represent taxonomic diversity. Despite SR not incorporating species abundance information, it remains a versatile, practical, and broadly comparable index for biodiversity valuation (Gaston & Spicer, 2003; Magurran, 2004). Thus, it is a fundamental metric in biodiversity studies due to its ease of comparison across regions and ability to provide baseline data for tracking ecological changes. The SR calculation was implemented in the 'specnumber' function from the 'vegan' R package [version 2.6-4; Oksanen *et al.* (2019)].

Phylogenetic richness (PD) was derived using Faith's PD, a widely accepted measure of diversity that calculates the evolutionary history of a set of taxa (represented as leaves) by summing the edge lengths connecting these taxa to the root of the tree (Faith, 1992), to represent phylogenetic diversity/richness. The index offers a straightforward interpretation of a community's evolutionary history, capturing the number of species and the evolutionary relationships and distances among them, thus offering insights into ecosystem resilience, feature diversity, and conservation priorities by valuing the breadth of evolutionary history. It has broad practical applications in ecology and evolutionary biology (Scherson & Faith, 2018). The PD calculation was implemented using the 'pd' function in the R package 'picante' [version 1.8.2; Kembel *et al.* (2010)].

Functional richness (FD) was estimated using the functional richness index of Villeger *et al.* (2008), i.e., the functional space volume occupied by the community. Unlike dendrogram-

240 based derivations of functional diversity, this approach's incorporation of trait
241 multidimensionality in terms of the species in a community and their combined trait space makes
242 it a more intuitive, flexible, and practical biodiversity index. The FD was calculated using the
243 'dbFD' function in R package 'FD' [version 1.0-12: Laliberté *et al.* (2014)].

244 *Net phylogenetic relatedness of species within communities* was represented by the
245 phylogenetic mean nearest taxon distance (PD^{MNTD}), estimating the average distance between
246 each species and its nearest relative in the community (Webb *et al.*, 2002; Webb & Donoghue,
247 2004). The PD^{MNTD} was calculated using the 'ses.mntd' function in R package 'picante' [version
248 1.8.2; Kembel *et al.* (2010)]. On the other hand, the *net functional relatedness of species within*
249 *communities* was represented by the functional mean nearest taxon distance (FD^{MNTD}), which
250 adopts the PD^{MNTD} concept to traits to estimate the mean distance of each species to its nearest
251 neighbor within the same community based on functional traits. This calculation is made
252 possible by using a distance matrix as input where the representation of species associations as
253 trees are first converted to a distance matrix. Thus, PD^{MNTD} captured the diversity of biological
254 traits present in a mountain community, emphasizing species' ecological roles, their interactions
255 with the environment and each other, and how these contribute to ecosystem functioning and
256 services. Its ability to identify functionally redundant or complementary species and reveal
257 functional clustering or overdispersion is vital to gaining ecological insights into species
258 persistence. The PD^{MNTD} was calculated analogously as PD^{MNTD} (using the 'ses.mntd' function
259 also in R package 'picante' [version 1.8.2; Kembel *et al.* (2010)]) following traits' conversion to
260 a trait distance matrix (Webb *et al.*, 2002; Webb *et al.*, 2008) using the Gower dissimilarity index
261 (Gower, 1971; Legendre & Legendre, 1998). Our use of MNTD generally relates to its
262 sensitivity to diversity at the finer branches of the phylogenetic tree or the smallest functional

differences between species, reflecting recent diversification events or niche differentiation. It provides unique insights into the evolutionary history of the community and helps to reveal patterns of phylogenetic clustering or overdispersion as it focuses on the phylogenetic or trait relationships between species. Thus, the resulting patterns may suggest the existence of environmental filtering pressures favoring related species with similar ecological traits or competitive exclusion limiting the success of closely related species living in close proximity. It is more sensitive to changes among closely related species or those with very similar functional traits, able to detect fine-scale ecological processes, informing the importance of preserving closely related species or those with unique functional traits.

Beta diversity: taxonomic, phylogenetic, and functional multisite beta diversity indices. To understand how variations in spatial grain influence biodiversity along elevational gradients, we partitioned beta diversity into its turnover and nestedness components across taxonomic, phylogenetic, and functional dimensions (Lozupone & Knight, 2005; Baselga, 2009; Baselga, 2012). We analyzed taxonomic beta diversity using a presence-absence dataset, quantifying species composition variation among sites. This approach helped us differentiate whether biodiversity changes were driven by species replacement (turnover) or by variations in species richness (nestedness-resultant components), enhancing our grasp of spatial scale impacts on community composition. Similarly, for phylogenetic beta diversity, we assessed changes in the phylogenetic makeup of communities using a phylogenetic tree, thereby determining if observed diversity shifts stemmed from phylogenetically similar or dissimilar species turnover or discrepancies in phylogenetic richness. This analysis elucidates the role of evolutionary histories in shaping community structures across diverse locales. In functional beta diversity, we investigated trait variation across sites to discern shifts in ecosystem functions attributable to

changes in species roles (functional turnover) versus alterations in the range of functions present (functional nestedness). By dissecting biodiversity components across spatial grains and landscapes, our work aims to deepen the understanding of biodiversity patterns and the underlying ecological and evolutionary processes. The analyses were implemented in the 'betapart' R package version 1.6: Baselga *et al.* (2018) using the Jaccard dissimilarity index and the community data matrix. The taxonomic beta diversity was implemented using the 'beta.multi' function, while phylogenetic beta diversity was implemented using the 'phylo.beta.multi' function, passing the phylogenetic tree as input. The functional beta diversity was computed using the 'phylo.beta.multi' function, passing the functional traits as arguments; however, the traits were first transformed by constructing a functional dendrogram using the 'hclust' function on the Gower distance matrix of traits, which was computed using the 'vegdist' function from the 'vegan' package. This dendrogram was then converted to a phylo object using the 'as.phylo' function.

List of References

Baker, B. (1967). *Geology of the Mount Kenya area* (Kenya Geological Survey, Geological Report, Issue.

Bartakova, V., Reichard, M., Janko, K., Polacik, M., Blazek, R., Reichwald, K., Cellerino, A., & Bryja, J. (2013). Strong population genetic structuring in an annual fish, Nothobranchius furzeri, suggests multiple savannah refugia in southern Mozambique. *BMC Evol Biol*, *13*, 196. doi: 10.1186/1471-2148-13-196

Barton, P. S., Cunningham, S. A., Manning, A. D., Gibb, H., Lindenmayer, D. B., & Didham, R. K. (2013). The spatial scaling of beta diversity [Article]. *Global ecology and biogeography*, *22*(6), 639-647. doi: 10.1111/geb.12031

Baselga, A. (2009). Partitioning the turnover and nestedness components of beta diversity. *Global ecology and biogeography*, *19*(1), 134-143. doi: 10.1111/j.1466-8238.2009.00490.x

Baselga, A. (2012). The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global ecology and biogeography*, *21*(12), 1223-1232. doi: 10.1111/j.1466-8238.2011.00756.x

Baselga, A., Orme, D., Villeger, S., De Bortoli, J., & Leprieur, F. (2018). *betapart: Partitioning Beta Diversity into Turnover and Nestedness Components. R package version 1.5.1*. In https://CRAN.R-project.org/package=betapart

Bennun, L. A., & Njoroge, P. (1999). *Important bird areas in Kenya*. Nature Kenya - The East Africa Natural History Society. https://doi.org/10.5962/bhl.title.87589

Brown, J., & Hay-Edie, T. (2014). World Heritage Papers. doi:

Bryja, J., Konvičková, H., Bryjová, A., Mikula, O., Makundi, R., Chitaukali, W. N., & Šumbera, R. (2018). Differentiation underground: Range-wide multilocus genetic structure of the silvery mole-rat does not support current taxonomy based on mitochondrial sequences. *Mammalian Biology*, *93*, 82-92. doi: 10.1016/j.mambio.2018.08.006

Burgess, N. D., Balmford, A., Cordeiro, N. J., Fjeldså, J., Küper, W., Rahbek, C., Sanderson, E. W., Scharlemann, J. P. W., Sommer, J. H., & Williams, P. H. (2007). Correlations among species distributions, human density and human infrastructure across the high biodiversity tropical mountains of Africa. *Biological Conservation*, *134*(2), 164-177. doi: 10.1016/j.biocon.2006.08.024

Cameron, A., Chege, B., Gachanja, M., Hofstede, M., Lambrechts, C., Powys, G., & Akinyi, J. (2000). Mount Elgon forest status report. doi:

Chorowicz, J. (2005). The East African rift system. *Journal of African Earth Sciences*, *43*(1-3), 379-410. doi: 10.1016/j.jafrearsci.2005.07.019

Davies, M. I. J. (2006). *The archaeology of the Cherangani Hills, Northwest Kenya* (0713-5815). U. K. St Hugh's College University of Oxford Oxford, OX.

de Klerk, H. M., Crowe, T. M., Fjeldså, J., & Burgess, N. D. (2002). Patterns of species richness and narrow endemism of terrestrial bird species in the Afrotropical region. *Journal of Zoology*, *256*(3), 327-342. doi: 10.1017/s0952836902000365

de la Sancha, N. U., Maestri, R., Bovendorp, R. S., & Higgins, C. L. (2020). Disentangling drivers of small mammal diversity in a highly fragmented forest system. *Biotropica*, *52*(1), 182-195. doi: 10.1111/btp.12745

Delvaux, D., & Khan, M. A. (1998). Tectonics, sedimentation and volcanism in the East African Rift System: introduction. *Journal of African Earth Sciences*, *26*(3), 343-346. doi: Doi 10.1016/S0899-5362(98)00019-0

Demos, T. C., Kerbis Peterhans, J. C., Joseph, T. A., Robinson, J. D., Agwanda, B., & Hickerson, M. J. (2015). Comparative Population Genomics of African Montane Forest Mammals Support Population Persistence across a Climatic Gradient and Quaternary Climatic Cycles. *PLoS ONE*, *10*(9), e0131800, Article e0131800. doi: 10.1371/journal.pone.0131800

Dianat, M., Voet, I., Ortiz, D., Goüy de Bellocq, J., Cuypers, L. N., Kryštufek, B., Bureš, M., Čížková, D., Bryjová, A., Bryja, J., Nicolas, V., & Konečný, A. (2023). Cryptic diversity of Crocidura shrews in the savannahs of Eastern and Southern Africa. *Molecular Phylogenetics and Evolution*, *180*, 107708. doi: https://doi.org/10.1016/j.ympev.2023.107708

Ebinger, C. (2005). Continental break-up: The East African perspective. *Astronomy & Geophysics*, *46*(2), 16-21. doi: DOI 10.1111/j.1468-4004.2005.46216.x

Engel, J. I., Byamana, K., Kahindo, C., Bates, J. M., Fjeldså, J., & Voelker, G. (2014). Genetic structure offers insights into the evolution of migration and the taxonomy of the Barred Long-tailed CuckooCercococcyx montanusspecies complex. *Ibis*, *156*(2), 330-340. doi: 10.1111/ibi.12145

Faith, D. P. (1992). Conservation Evaluation and Phylogenetic Diversity. *Biological Conservation*, *61*(1), 1-10. doi: Doi 10.1016/0006-3207(92)91201-3

Foster, D. A., & Gleadow, A. J. (1992). The morphotectonic evolution of rift-margin mountains in central Kenya: constraints from apatite fission-track thermochronology. *Earth and Planetary Science Letters*, *113*(1-2), 157-171. doi:

Furman, T., Nelson, W. R., & Elkins-Tanton, L. T. (2016). Evolution of the East African rift: Drip magmatism, lithospheric thinning and mafic volcanism. *Geochimica Et Cosmochimica Acta*, *185*, 418-434. doi: 10.1016/j.gca.2016.03.024

Gaston, K. J., & Spicer, J. I. (2003). *Biodiversity: An Introduction, 2nd Edition*. Blackwell Science Ltd.

Gichuki, F. N. (1999). Threats and opportunities for mountain area development in Kenya. *Ambio*, *28*(5), 430-435. doi: <Go to ISI>://WOS:000082807300007

Gower, J. C. (1971). A general coefficient of similarity and some of its properties. *Biometrics*, *27*(4), 857-871. doi: 10.2307/2528823

Hastenrath, S., & Kruss, P. D. (1992). THE DRAMATIC RETREAT OF MOUNT KENYA GLACIERS BETWEEN 1963 AND 1987 - GREENHOUSE FORCING. In R. L. Hooke (Ed.), *Annals of Glaciology, Vol 16, 1992: Proceedings of the Symposium on Mountain Glaciology Relating to Human Activity* (Vol. 16, pp. 127-133). <Go to ISI>://WOS:A1992BX22L00021

Haug, G. H., & Strecker, M. R. (1995). Volcano-Tectonic Evolution of the Chyulu Hills and Implications for the Regional Stress-Field in Kenya. *Geology*, *23*(2), 165-168. doi: Doi 10.1130/0091-7613(1995)023<0165:Vteotc>2.3.Co;2

Hedberg, O. (1969). Evolution and speciation in a tropical high mountain flora. *Biological Journal of the Linnean Society*, *1*(1-2), 135-148. doi: 10.1111/j.1095-8312.1969.tb01816.x

Hopp, J., Trieloff, M., & Altherr, R. (2007). Noble gas compositions of the lithospheric mantle below the Chyulu Hills volcanic field, Kenya. *Earth and Planetary Science Letters*, *261*(3-4), 635-648. doi: 10.1016/j.epsl.2007.07.027

Hughes, D. F., Tolley, K. A., Behangana, M., Lukwago, W., Menegon, M., Dehling, J. M., Stipala, J., Tilbury, C. R., Khan, A. M., Kusamba, C., & Greenbaum, E. (2018). Cryptic diversity in Rhampholeon boulengeri (Sauria: Chamaeleonidae), a pygmy chameleon from the Albertine Rift biodiversity hotspot. *Mol Phylogenet Evol*, *122*, 125-141. doi: 10.1016/j.ympev.2017.11.015

Jacquet, F., Denys, C., Verheyen, E., Bryja, J., Hutterer, R., Kerbis Peterhans, J. C., Stanley, W. T., Goodman, S. M., Couloux, A., Colyn, M., & Nicolas, V. (2015). Phylogeography and evolutionary history of the Crocidura olivieri complex (Mammalia, Soricomorpha): from a forest origin to broad ecological expansion across Africa. *BMC Evol Biol*, *15*, 71, Article 71. doi: 10.1186/s12862-015-0344-y

Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P., & Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, *26*(11), 1463-1464. doi: 10.1093/bioinformatics/btq166

Korner, C., & Spehn, E. M. (Eds.). (2019). *Mountain Biodiversity: A Global Assessment*. The Parthenon Publishing Group [Routledge].

Küper, W., Sommer, J. H., Lovett, J. C., Mutke, J., Linder, H. P., Beentje, H. J., Van Rompaey, R. S. A. R., Chatelain, C., Sosef, M., & Barthlott, W. (2004). Africa's hotspots of biodiversity redefined. *Annals of the Missouri Botanical Garden*, *91*(4), 525-535. doi: <Go to ISI>://WOS:000226362700001

Laliberté, E., Legendre, P., & Shipley, B. (2014). *FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12.* In https://cran.r-project.org/web/packages/FD/index.html

Lambrechts, C., Woodley, B., Church, C., & Gachanja, M. (2003). Aerial survey of the destruction of the Aberdare Range forests. *Division of Early Warning and Assessment, UNEP*. doi:

Legendre, P., & Legendre, L. (1998). *Numerical ecology* (Second English ed.). Elsevier.

Leitner, W. A., & Rosenzweig, M. L. (1997). Nested species-area curves and stochastic sampling: A new theory. *Oikos*, *79*(3), 503-512. doi: Doi 10.2307/3546894

Loomis, S. E., Russell, J. M., Verschuren, D., Morrill, C., De Cort, G., Sinninghe Damste, J. S., Olago, D., Eggermont, H., Street-Perrott, F. A., & Kelly, M. A. (2017). The tropical lapse rate steepened during the Last Glacial Maximum. *Sci Adv*, *3*(1), e1600815, Article e1600815. doi: 10.1126/sciadv.1600815

Lozupone, C., & Knight, R. (2005). UniFrac: a new phylogenetic method for comparing microbial communities. *Appl Environ Microbiol*, *71*(12), 8228-8235. doi: 10.1128/AEM.71.12.8228-8235.2005

Lusigi, W. J. (1989). A case study of the Mt. Kulal Biosphere Reserve. Worldwide Conservation: Proceedings of the Symposium on Biosphere Reserves,

Mäckel, R., Schultka, W., & Walther, D. (2021). THE PHYSICAL ENVIRONMENT OF MOUNT KULAL. *Quaternary and Environmental Research on East African Mountains*, 405. doi:

Magurran, A. E. (2004). *Measuring biological diversity*. Blackwell Publishing.

Mahaney, W. C., Krinsley, D. H., Allen, C. C. R., Langworthy, K., Ditto, J., & Milner, M. W. (2012). Weathering Rinds: Archives of Paleoenvironments on Mount Kenya, East Africa. *The Journal of Geology*, *120*(6), 591-602. doi: 10.1086/667805

Mairal, M., Sanmartin, I., Herrero, A., Pokorny, L., Vargas, P., Aldasoro, J. J., & Alarcon, M. (2017). Geographic barriers and Pleistocene climate change shaped patterns of genetic variation in the Eastern Afromontane biodiversity hotspot [Article]. *Sci Rep*, *7*, 45749. doi: 10.1038/srep45749

Males, J., Neate-Clegg, M. H. C., & Tingley, M. W. (2023). Building a mechanistic understanding of climate-driven elevational shifts in birds. *PLOS Climate*, *2*(3), e0000174. doi: 10.1371/journal.pclm.0000174

Mamantov, M. A., Gibson-Reinemer, D. K., Linck, E. B., & Sheldon, K. S. (2021). Climate-driven range shifts of montane species vary with elevation. *Global ecology and biogeography*, *30*(4), 784-794. doi: 10.1111/geb.13246

Maslin, M. A., Brierley, C. M., Milner, A. M., Shultz, S., Trauth, M. H., & Wilson, K. E. (2014). East African climate pulses and early human evolution. *Quaternary Science Reviews*, *101*(-), 1-17. doi: 10.1016/j.quascirev.2014.06.012

Mazoch, V., Mikula, O., Bryja, J., Konvičková, H., Russo, I.-R., Verheyen, E., & Šumbera, R. (2018). Phylogeography of a widespread sub-Saharan murid rodent Aethomys chrysophilus: the role of geographic barriers and paleoclimate in the Zambezian bioregion. *mammalia*, *82*(4), 373-387. doi: 10.1515/mammalia-2017-0001

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends Ecol Evol*, *21*(4), 178-185. doi: 10.1016/j.tree.2006.02.002

Morley, C., Harper, R., & Wigger, S. (1999). Introduction to the East African Rift System. In C. Morley (Ed.), *Geoscience of Rift Systems—Evolution of East Africa: AAPG Studies in Geology* (Vol. 44, pp. 1-18). American Association of Petroleum Geologists.

Morley, C. K., Ngenoh, D. K., & Ego, J. K. (1999). Introduction to the East African Rift System. In C. K. Morley (Ed.), *Geoscience of Rift Systems—Evolution of East Africa: AAPG Studies in Geology* (Vol. 44, pp. 1-18).

Murungi, M. L., McGlynn, G., & Lejju, J. B. (2017). Alpine grassland palaeoecology of the Virunga Volcanoes, East Africa: A new phytolith record from Mt. Muhavura. *Quaternary International*, *434*, 102-116. doi: 10.1016/j.quaint.2016.01.015

Musila, S., Chen, Z. Z., Li, Q., Yego, R., Zhang, B., Onditi, K., Muthoni, I., He, S. W., Omondi, S., Mathenge, J., Kioko, E. N., & Jiang, X. L. (2019). Diversity and distribution patterns of non-volant small mammals along different elevation gradients on Mt. Kenya, Kenya. *Zool Res*, *40*(1), 53-60. doi: 10.24272/j.issn.2095-8137.2019.004

Neumann, F. H., & Scott, L. (2018). E.M. van Zinderen Bakker (1907–2002) and the study of African Quaternary palaeoenvironments. *Quaternary International*, *495*, 153-168. doi: 10.1016/j.quaint.2018.04.017

Nicolas, V., Mboumba, J.-F., Verheyen, E., Denys, C., Lecompte, E., Olayemi, A., Missoup, A. D., Katuala, P., & Colyn, M. (2008). Phylogeographic Structure and Regional History of Lemniscomys striatus (Rodentia:

Muridae) in Tropical Africa. *Journal of Biogeography*, *35*(11), 2074-2089. doi: www.jstor.org/stable/20143424

Nield, R., Mugo, E., & Mwathe, K. (2000). Review of the management of the forest resources of the Mt. Elgon ecosystem. doi:

Nonnotte, P., Guillou, H., Le Gall, B., Benoit, M., Cotten, J., & Scaillet, S. (2008). New K–Ar age determinations of Kilimanjaro volcano in the North Tanzanian diverging rift, East Africa. *Journal of Volcanology and Geothermal Research*, *173*(1-2), 99-112. doi: 10.1016/j.jvolgeores.2007.12.042

Novak, O., Prodehl, C., Jacob, A. W. B., & Okoth, W. (1997a). Crustal structure of the southeastern flank of the Kenya rift deduced from wide-angle P-wave data. *Tectonophysics*, *278*(1-4), 171-186. doi: 10.1016/s0040-1951(97)00100-5

Novak, O., Ritter, J. R. R., Altherr, R., Garasic, V., Volker, F., Kluge, C., Kaspar, T., Byrne, G. F., Sobolev, S. V., & Fuchs, K. (1997b). An integrated model for the deep structure of the Chyulu Hills volcanic field, Kenya. *Tectonophysics*, *278*(1-4), 187-209. doi: 10.1016/S0040-1951(97)00104-2

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2019). *vegan: Community Ecology Package. R package version 2.5-5.* In https://CRAN.R-project.org/package=vegan

Onditi, K. O., Song, W. Y., Li, X. Y., Chen, Z. Z., Li, Q., He, S. W., Musila, S., Kioko, E., & Jiang, X. L. (2022). Patterns and Predictors of Small Mammal Phylogenetic and Functional Diversity in Contrasting Elevational Gradients in Kenya [Original Research]. *Frontiers in Ecology and Evolution*, *9*(964), 742524. doi: 10.3389/fevo.2021.742524

Ongugo, P., Njguguna, J., Obonyo, E., & Sigu, G. (2002). Livelihoods, natural resource entitlements and protected areas: the case of Mt. Elgon forest in Kenya. *Kenya IFRI Collaboratve Research Centre.[Online] Available at: http://www. cbd. int/doc/case-studies/for/cs-ecofor-ke-02-en. pdf. Accessed on*, *12*(01), 2013. doi:

Prodehl, C., Ritter, J. R. R., Mechie, J., Keller, G. R., Khan, M. A., Jacob, B., Fuchs, K., Nyambok, I. O., Obel, J. D., & Riaroh, D. (1997). The KRISP 94 lithospheric investigation of southern Kenya — the experiments and their main results. *Tectonophysics*, *278*(1-4), 121-147. doi: 10.1016/s0040-1951(97)00098-x

R Core Team. (2024). *R: A Language and Environment for Statistical Computing*. In R Foundation for Statistical Computing. https://www.R-project.org/

Rotich, B. (2019). Forest Conservation and Utilization in Embobut, Cherangani Hills, Kenya. *International Journal of Natural Resource Ecology and Management*, *4*(1). doi: 10.11648/j.ijnrem.20190401.12

Scheiner, S. M. (2003). Six types of species-area curves. *Global ecology and biogeography*, *12*(6), 441-447. doi: DOI 10.1046/j.1466-822X.2003.00061.x

Scherson, R., & Faith, D. P. (Eds.). (2018). *Phylogenetic Diversity: Applications and Challenges in Biodiversity Science*. Springer. https://doi.org/10.1007/978-3-319-93145-6.

Schüler, L., Hemp, A., & Behling, H. (2014). Relationship between vegetation and modern pollen-rain along an elevational gradient on Kilimanjaro, Tanzania. *The Holocene*, *24*(6), 702-713. doi: 10.1177/0959683614526939

Sumbera, R., Krasova, J., Lavrenchenko, L. A., Mengistu, S., Bekele, A., Mikula, O., & Bryja, J. (2018). Ethiopian highlands as a cradle of the African fossorial root-rats (genus Tachyoryctes), the genetic evidence. *Mol Phylogenet Evol*, *126*, 105-115. doi: 10.1016/j.ympev.2018.04.003

Taylor, P. J., Maree, S., Van Sandwyk, J., Kerbis Peterhans, J. C., Stanley, W. T., Verheyen, E., Kaliba, P., Verheyen, W., Kaleme, P., & Bennett, N. C. (2009). Speciation mirrors geomorphology and palaeoclimatic history in African laminate-toothed rats (Muridae: Otomyini) of the Otomys denti and Otomys lacustris species-complexes in the 'Montane Circle' of East Africa. *Biological Journal of the Linnean Society*, *96*(4), 913-941. doi: j.1095-8312.2008.01153.x

Vedeld, P., Rooij, A. v., Sundnes, F., & Jørgensen, I. T. (2005). Final appraisal of the Mt. Elgon Regional Ecosystem Conservation Programme (MERECP). doi:

Veldkamp, A., Buis, E., Wijbrans, J. R., Olago, D. O., Boshoven, E. H., Marée, M., & van den Berg van Saparoea, R. M. (2007). Late Cenozoic fluvial dynamics of the River Tana, Kenya, an uplift dominated record. *Quaternary Science Reviews*, *26*(22-24), 2897-2912. doi: 10.1016/j.quascirev.2007.06.033

Veldkamp, A., Schoorl, J. M., Wijbrans, J. R., & Claessens, L. (2012). Mount Kenya volcanic activity and the Late Cenozoic landscape reorganisation in the upper Tana fluvial system. *Geomorphology*, *145*, 19-31. doi: 10.1016/j.geomorph.2011.10.026

Villeger, S., Mason, N. W., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, *89*(8), 2290-2301. doi: 10.1890/07-1206.1

Voelker, G., Huntley, J. W., Bryja, J., Denys, C., Šumbera, R., Demos, T. C., Lavrenchenko, L., Nicolas, V., Gnoske, T. P., & Kerbis Peterhans, J. C. (2021). Molecular systematics and biogeographic history of the African climbing-mouse complex (Dendromus). *Molecular Phylogenetics and Evolution*, 107166. doi: https://doi.org/10.1016/j.ympev.2021.107166

Webb, C. O., Ackerly, D. D., & Kembel, S. W. (2008). Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics*, *24*(18), 2098-2100. doi: 10.1093/bioinformatics/btn358

Webb, C. O., Ackerly, D. D., McPeek, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual review of Ecology and Systematics*, *33*(1), 475-505. doi: 10.1146/annurev.ecolsys.33.010802.150448

Webb, C. O., & Donoghue, M. J. (2004). Phylomatic: tree assembly for applied phylogenetics. *Molecular ecology notes*, *5*(1), 181-183. doi: 10.1111/j.1471-8286.2004.00829.x

Western, D., Musyoki, C., Mwangi, E., Mwachala, G., Said, M., Wargute, P., Matiku, P., Landsberg, F., Kamala, E., Waruingi, L., Kariuki, P., Situma, C., Ojwang, G., Njino, L., Mulenkei, L., Muli, D., Malombe, I., Marchant, R., Platts, P., & Stickler, M. (2015). *Kenya's Natural Capital: A Biodiversity Atlas*. Ministry of Environment Natural Resources and Regional Development Authorities, Kenya. https://biodiversityatlaskenya.org/reports/

Wichura, H., Bousquet, R., Oberhänsli, R., Strecker, M. R., & Trauth, M. H. (2010). Evidence for middle Miocene uplift of the East African Plateau. *Geology*, *38*(6), 543-546. doi: 10.1130/G31022.1