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A Decade-Long Change in the Elevational Distribution of Non-Volant Small Mammals on Mount Meru, Tanzania

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Abstract: Understanding species distribution across elevational gradients is crucial for developing conservation strategies for montane biotic systems. A survey of small mammals was conducted on Mount Meru at six elevations, ranging between 1500 m and 3650 m. A total of 803 small mammal individuals, including 2 shrew species and 13 rodent species, were documented. Of these, *Crocidura newmarki* and *Lophuromys verhageni* were endemic on Mount Meru. Species richness was highest at mid–elevations, which is in line with the global pattern for small mammals. Prior to our study, the most complete data on small mammals on Mount Meru was collected in 2009. Our study provides an opportunity to show how small mammal elevational distribution has changed, over the last decade. We found six species (*Arvicanthis niloticus*, *Mastomys natalensis*, *Lemniscomys striatus*, *Dasymys incomtus*, *Cricetomys ansorgei*, and *Montemys delectorum*), which were not documented in 2009, but did not find *Otomys tropicalis*. Interestingly, the community composition at higher elevations in 2021 resembles that at lower elevations in 2009, suggesting that small mammal species have moved their range upward over time. Climate change could be a factor associated with the distributional shift found.

Keywords: elevational distribution; rodents; shrews; species composition; climate changes

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1. Introduction

Tropical mountains are key habitats for biodiversity; they harbour a high level of species richness and endemism [1,2]. However, due to climate change, ecological disturbances, and other human–induced changes, montane species are, increasingly, under threat [3–5]. Understanding the distribution of montane species along an elevational gradient enables the development of conservation strategies and foresees species's responses to future environmental changes [6–8]. Over the last decades, there has been an increase in studies that document the elevational distribution of small mammals worldwide (China [6], Ethiopia [9], Peru [10], Philippines [11,12], Slovakia [13], Romania [14], the USA [15], and Tanzania [16,17]). The understanding of specific and general patterns of mammalian elevational distribution provided by these studies is noteworthy, and it serves as a vital benchmark for assessing the effect of environmental change over time. For instance, Craig et al. [9] recently revealed that changes in climate have resulted in in upward elevational changes in the ranges of rodent and shrew species in Simien Mountains National Park, Ethiopia, after 88 years.

Many East African mountain ranges have been the focus of research on the elevational distribution of small animals, including Mount Elgon in Uganda [18,19], Simien Mountain

National Parks in Ethiopia [9], Mount Kenya in Kenya [20], and the Udzungwa [21] and Kilimanjaro mountains in Tanzania [16,17]. There are, of course, other topographically important massifs that have attracted less scientific attention.

Mount Meru (4566 m) is the second highest mountain in Tanzania, after Kilimanjaro, and the centrepiece of Arusha National Park. The high diversity of landscapes, from open grassland to montane and Afroalpine forests, are home to a highly diverse wildlife community [22]. The lower and central slopes are particularly broad and provide a potential refuge, for a great array of large mammalian fauna [23]. Small mammals, including rodents and shrews, are, also, important components of this mountain ecosystem, where they play a vital role in the distribution and abundance of other animal taxa through top–down and bottom–up control. Meanwhile, they function as soil aerators, pollinators, and seed dispersers [24]. Despite their key contribution to the ecosystem, very little is known about them on Mount Meru.

The first reports of small mammal fauna on Mount Meru are those of Demeter and Hutterer [25], who provided scattered records of species occurrence, mainly from the lower altitudes. Only Stanley and Kihaule [26], in 2009, employed a systematic survey to document small–mammal distribution along elevational gradients in the study area. Updated and more detailed information about this ecosystem is, therefore, required, since, as the climate changes over time, so does the distribution of species [27]. Resurveys of small mammals across the world have revealed elevational shifts in species ranges, in response to climate change [9,15,28]. However, we found limited references in Africa. We, therefore, sought to: (i) determine the current elevational distribution and diversity of small mammal species and (ii) compare our findings to those from the 2009 survey [26], to assess community composition changes over time along an elevational gradient.

2. Materials and Methods

2.1. Study Area

The study was conducted on Mount Meru (3°14′48″ and 36°44′54″), located in the northeastern part of Tanzania, about 35 km northeast of Arusha town (Figure 1). The topography is, generally, rugged, as a result of historical volcanic activity, and rises from the Momela Lakes (northeast) and Ngurdoto crater (southeast), lying at 1400 m, to the Meru crater and summit (west end), at 4566 m. The rainfall pattern is bimodal and varies with the altitude. The short rain period occurs between October and December, and the long rainy season is between March and May. The dry season is from June to September. In lower, drier areas, annual rainfall ranges between 600 mm and 1300 mm, and at 2590 m a.s.l. in the Meru crater, between 1400 mm and 2400 mm [23].

2.2. Sampling Sites and Vegetation Types

There is a single path, which provides access to climbers from the lowlands, and runs up the southeastern slope of the massif. Six sites were sampled for small mammals, between February and November 2021, along this route, with an elevation ranging from roughly 1500–3650 m a.s.l. Sites were selected based on altitude and the major vegetation type. Each site and elevation was centered at the corresponding campsite. Details on habitat notes related to each site, trapping altitude, coordinates, and date of sampling are given below (representative habitats photographed at each site are provided in Figure 2). Vegetation identification in each site was based on [29,30]. All sampling sites span along the Arusha National Park.

Savanna (SA): 1500 m; 3°13′20.766″ S, 36°52′50.076″ E; 11–16 February 2021. This site is located at the foot of Mount Meru. The vegetation cover of this site varies from grassland, thicket, and bushland to woodland. The conspicuous plant species include C*aesalpinia decapetala*, *Croton macrostachyus*, *Jacaranda mimosifolia*, *Senna spectabilis*, *Ocimum gratissimum*, O*rthosiphon parvifolius*, *Solanum incanum*, *Aerva lanata*, *Lantana trifolia*, and tussock grasses. Scattered patches of *Acacia xanthophloea* trees are, also, common on this site.

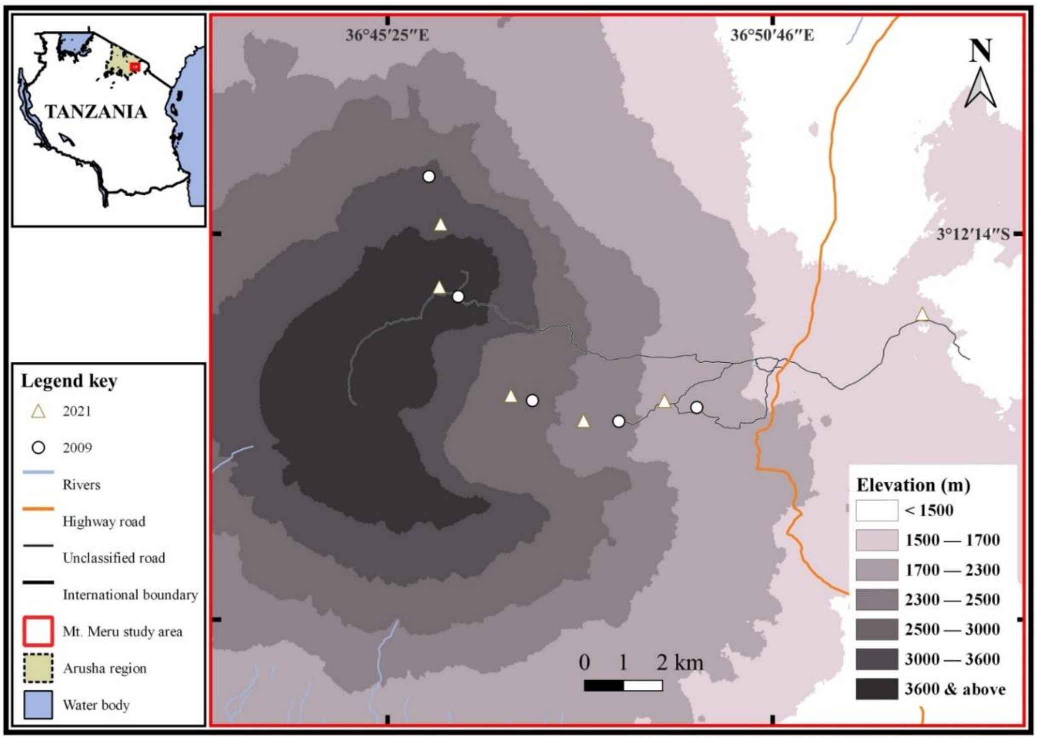

Figure 1. Map of Mount Meru, Tanzania, showing sampling points. Symbols indicate trapping elevations for 2009 (circle) and 2021 (triangle) studies. Elevation zones are represented with color in the legend.

Lower montane forest (LMF): 2000 m; 3°14′33.102″ S, 36°49′15.528″ E; 4–9 July 2021. This site is in a lower montane forest, with a closed canopy of tall and medium–height trees of various species, such as *Diospyros abyssinica*, *Olea hochstetteri*, *Rhamnus prinoides*, *Ficus thonningii*, *Nuxia*, and *Podocarpus*.

Upper montane forest (UMF): 2500 m; 3°14′32.892″ S, 36°47′25.644″ E; 4–9 July 2021. This site is positioned in the upper montane forest dominated by *Juniperus procera and Podocarpus gracilior*, which is followed by a small band of cloud forest with *Hagenia abyssinica.* In much of this type of forest, there was dense undergrowth of herbaceous plants, lianas of different species, and shrubs, and the trees were festooned with epiphytes. Mosses were common on dead wood and live trees. The site, also, included rivers and swamp areas that were rounded off by Papyrus and Miscanthusas plant species.

Upper montane forest/Ericaceous heath (UMF/EH); 2950 m: 3°13′28.724″ S, 36°47′7.782″ E; 3–8 August 2021. This site is located in a transitional zone between upper montane forest and ericaceous heath habitats, conquered by *Hagenia abyssinica*, *Erica arborea*, *Stoebe kilimandscharica*, and some *Lobelia* species.

Ericaceous heath (EH); 3500 m: 3°13′6.192″ S, 36°46′24.042″ E; 3–8 August 2021. This site was situated in the ericaceous heathland, where *Erica reunionensis*, *Pennisetum setaceum*, *and Santolina* species dominated the habitat. The majority of the forests on this site were dried, due to the experienced firebreak.

Afroalpine (AA); 3650 m: 3°12′6.193″ S, 36°46′9.294″ E; 11–16 November 2021. This highest point is in the Afroalpine zone. Tussock grass and some scrubs were found on this site.

Figure 2. Photographs of representative habitats for each site sampled on Mount Meru, Tanzania. SA (savanna grassland), LMF (lower montane forest), UMF (upper montane forest), UMF/EH (upper montane forest/Ericaceous heathland), EH (ericaceous heathland), and AA (Afroalpine).

2.3. Trapping Techniques and Identification

The trapping of small mammals was carried out in trap lines, consisting of medium–sized Sherman, 7.5 × 9 × 23 cm (H.B. Sherman Traps Inc., Tallahassee, FL, USA), and Havahart traps. At the SA, LMF, UMF, and UMF/EH, four trap lines were established, each with 50 traps. In the EH and AA sites, a total of 38 Sherman traps only were employed in five trap lines. The trap lines in all sites were established from 30 m to 50 m apart, as described in the literature, with trap stations spaced up to 10 m apart, with one trap per station. There were six days of sampling at each site, accumulating a total of 1140–1200 trap nights (Table 1). The Sherman traps were baited, using peanut butter mixed with maize flour and avocado, whereas the Havahart traps were baited with a combination of fresh banana, green maize, and avocado. Traps were inspected every morning at 07:00–08:00 h and rebaited. Animals were euthanized with Diethyl ether, using a piece of cotton wool, in the temporary laboratory in the field, and handled following the ethical policies and guidelines approved by the committee for Animal Care and Use of Sokoine University of Agriculture. For each representative species, muscle/or kidney tissues were preserved, in 96% ethanol, for further research. For all trapped animals, standard external body measurements (body, tail, hindfoot, and left ear) and weight were recorded. This study considered only non–flying small mammals, including shrews and rodents. Animals were handled following the guidelines of the American Society of Mammalogists [31]. Each captured species was identified in the field, using distributional data from Happold [32], Stanley and Kihaule [26], and experts from Sokoine University of Agriculture's Institute of Pest Management. Representative samples for each species are kept at the Institute of Pest Management, Sokoine University of Agriculture, Tanzania.

2.4. Data Analysis

We compiled the number of individuals of each small mammal species per site and calculated the sampling effort in terms of trap nights. Unequal trapping effort among sites was accounted for, by using as a measure of species abundance a capture index, i.e., trap success. We calculated percentage of trap success, by dividing the number of individuals caught by the number of trap nights (i.e., the number of traps used, multiplying by number of trapping days) and multiplying by 100. A trap night is defined as a single trap set for 24 h. Species composition is given by the relative abundances of species, i.e., their proportions within the assemblage. A linear regression model was used to test the relationship between species relative abundance and elevation. To assess completeness of sampling, we generated species accumulation curves and calculated estimated species richness, using Estimate S version 9.1.0 [33]. We used the Chao non–parametric estimator, to estimate the number of missing species in the overall survey pool. For individual sites, species richness was estimated, using the Abundance Coverage Estimator (ACE), due to its capability to knob species abundance data with low observed richness. Diversity and evenness were, also, calculated for each site. To evaluate species diversity, we used the Shannon diversity index, H' [34], and derived evenness, E (H'/lnS), to show how the species are distributed in the community.

2.5. Analysing and Comparing the 2009 and 2021 Surveys

We compared the present elevational distribution of small mammals with prior surveys on Mount Meru, using a diversity and distribution dataset collected by William T. Stanley and Philip M. Kihaule in 2009 (hereafter, 2009 survey) and published in 2016 [26]. Between 16 July 2009 and 19 August 2009, the authors surveyed small mammals at five different elevations (1950 m, 2300 m, 2650 m, 3000 m, and 3600 m) along the southeastern aspect of Mount Meru using Sherman traps, Victor Rat traps, Museum Special traps, and pitfall buckets. Bait for each trap consisted of freshly fried coconut coated in peanut butter. We used the generated species distribution and abundance data of the 2009 survey to determine small mammal distributions, for each site over time. To account for the inconsistency in the trapping efforts between the two surveys, the species's trap success and percentage of relative abundance were used for comparison. The absolute abundances for both studies are given in Appendix A Table A1. All of the 2009 small mammal data, on which our study was based, are publicly available [26]. All the sites sampled in 2009 were included within the boundary of our survey. To make direct comparisons between the 2009 and 2021 surveys, sites from both surveys were consolidated into six elevational sampling bands. The elevational zone is established, based on the major vegetation belts of Mount Meru: (a) savanna (SA; 1500–1700 m; this site was not surveyed in the 2009 study), (b) lower montane forest (LMF; 1700–2300 m), (c) upper montane forest (UMF; 2300–2550 m), (d) upper montane forest/ericaceous heathland (UMF/EH; 2550–3000 m), (e) ericaceous heathland (EH; 3000–3600 m), and (f) Afroalpine (AA; 3600 m and above) [29]. QGIS software was used to create these digital elevation models of the study sites.

To assess changes in small mammal community composition for each site and time period, we conducted a Principal Coordinate Analysis (PCoA) using a Paleontological Statistics Software (PAST) Package. The Bray–Curtis dissimilarity matrix was used to quantify the compositional dissimilarity within each zone, between the two surveys. A paired t–test was used to compare the distribution of sites between the 2009 and 2021 surveys along the first major axis. To estimate changes in climate between the two surveys, we downloaded 43 years (1979–2021) of historical climate data from Arusha National Park, the core of Mount Meru, from the data source ERA5, the fifth–generation ECMWF atmospheric reanalysis of global climate, with a spatial resolution of 30 km [35]. We converted the yearly data to about 10–year averages (1979–1988, 1989–1998, 1999–2008, and 2009–2021), and the average mean temperature for each interval was calculated, to determine the mean increase temperature per decade. We regressed the annual mean temperature against the year for a period of 43 years, to see the trend of changing temperatures over time. Changes in climate over time were evaluated with simple linear regression, where the year was used as an explanatory variable and the yearly mean temperature variable as a response.

3. Results

3.1. Abundance and Species Richness across Elevation Graident

We recorded 803 small mammal captures in 7080 trap nights, with a total trap success of 11.3%, ranging from 4.5% to 21.9%. Of the small mammals captured, 595 were rodents (Rodentia) and 208 were shrews (Insectivora). While rodents belonged to 13 species under 12 genera, the shrews belonged to 2 species under 1 genus (Table 1). Only two of the species (*Lophuromys verhageni* and *Crocidura newmarki*) were endemic to the study area. *Praomys taitae* was the most abundant species, with 40% ($n = 321$) contribution of the total small mammals. *Crocidura newmarki* was the second most abundant species, with a percentage of relative abundance of 15.8% ($n = 127$). *Mus triton* 0.5% ($n = 4$), *Lemniscomys striatus* 0.5 % ($n = 4$), and *Montemys delectorum* 0.4% ($n = 3$) were the three most infrequently captured species. In the SA sites, *Mastomys natalensis* was the most abundant, accounting for 51.8% of the total individual in the habitat, where as in the LMF and UMF, *Praomys taitae* were the dominant species, with 57.1% and 73.0%, respectively, for each site. As for the EH, *Crocidura* species and *Lophuromys verhageni* were frequent. A linear regression model of species richness, total percentage of trap success, and total percent contribution in relation to elevation were not significant (all $p > 0.05$). The chi–squared (X^2) analysis results in Table 2 show that the species composition of small mammals in all habitats were significantly different ($p < 0.05$), except the UMF/EH ($X^2 = 6.27$, df = 10, $p = 0.134$).

Table 1. Percentage contribution and total abundance (in parentheses) of small mammals in different sites on Mount Meru.

	Sites						
	SA	**LMF**	**UMF**	**UMF/EH**	**EH**	**AA**	**Totals**
Rodents							
Rhabdomys dilectus	3.6(2)	0.8(1)	1.1(3)	17.4(26)	12.7(20)	70.6(36)	11.0(88)
Praomys taitae	–	57.1(72)	73.0(192)	26.2(39)	11.4(18)	–	40.0(321)
Montemys delectorum [@]	–	–	0.8(2)	0.7(1)	–	–	0.4(3)
Mus triton	–	–	–	–	–	7.8(4)	0.5(4)
Mastomys natalensis	51.8(29)	–	–	–	–	–	3.6(29)
Lophuromys verhageni	–	–	–	8.1(12)	23.4(37)	9.8(5)	6.7(54)
Lemniscomys striatus	–	–	1.1(3)	0.7(1)	–	–	0.5(4)
Graphiurus murinus	–	–	–	14.1(21)	3.2(5)	–	3.2(26)
Grammomys dolichurus	10.7(6)	2.4(3)	1.9(5)	2.7(4)	1.9(3)	–	2.6(21)
Dendromus insignis	–	–	–	–	2.5(4)	5.9(3)	0.9(7)
Dasymys incomtus	–	2.4(3)	1.1(3)	0.7(1)	–	–	0.9(7)
Cricetomys ansorgei	–	3.2(4)	1.1(3)	1.3(2)	¥	¥	1.1(9)
Arvicanthis niloticus	30.4(17)	4(5)	–	–	–	–	2.7(22)
Shrews							
Crocidura newmarki	3.6(2)	30.2(38)	7.2(19)	15.4(23)	26.6(42)	5.9(3)	15.8(127)
Crocidura allex	–	–	12.5(33)	12.8(19)	29(18.4)	–	10.1(81)
Rodent abundance	96.4(54)	69.8(88)	80.2(211)	71.80(107)	55.1(87)	94.1(48)	74.1(595)
Shrew abundance	3.6(2)	30.2(38)	19.8(52)	28.2(42)	44.9(71)	5.9(3)	25.9(208)
Rodent species	4	6	7	9	6	4	13
Shrew species	1	1	2	2	2	1	2
Trap success (%)	4.7	10.5	21.9	12.4	13.9	4.5	11.3
Trap effort	1200	1200	1200	1200	1140	1140	7080

[@] *As Praomys delectorum* in previous studies (but see Nicolas et al., 2021) "–"Not recorded; ¥ Not assessed. SA (savanna); LMF (lower montane forest); UMF (upper montane forest); UMF/EH (upper montane forest/Ericaceous heathland); EH (ericaceous heathland); and AA (Afroalpine).

Table 2. Chi–squared (X^2) statistical results of species composition in each sites.

	SA	LMF	UMF	UMF/EH	EH	AA
X^2	27.00	22.87	15.00	6.27	19.20	27.00
df	5	7	9	10	8	5
p–value	**0.000**	**0.001**	**0.035**	0.134	**0.003**	**0.00**

SA (savanna); LMF (lower montane forest); UMF (upper montane forest); UMF/EH (upper montane forest/Ericaceous heathland); EH (ericaceous heathland); and AA (Afroalpine). Bold indicates statistically significant.

Our results show that the distribution of species varies between sites (Table 3). The percentage of relative abundance of *Rhabdomys dilectus* and *Mus triton* was higher in the AA, whereas *Lophuromys verhageni*, *Crocidura newmarki*, and *Dendromus insignis* showed higher percentage of relative abundance in the EH. For *Graphiurus murinus*, 80.8% of the total was found in the UMF/EH. *Praomys taitae*, *Montemys delectorum*, and *Lemniscomys striatus* were highest in the UMF habitat. *Dasymys incomtus* and *Cricetomys ansorgei* were recorded in the LMF. In addition, high abundances of *Mastomys natalensis* (100%), *Arvicanthis niloticus*, and *Grammomys dolichurus* were recorded in the SA habitats. Based on the result of a linear regression model, the distribution of *Rhabdomys dilectus* showed a strong positive relationship with elevation ($R^2 = 0.89$, $p = 0.016$). The distribution of *Dendromus insignis* was, also, strongly related with elevation ($R^2 = 0.80$, $p = 0.05$). Similarly, the association between *Arvicanthis niloticus* and elevation was strong ($R^2 = -0.78$, $p = 0.04$) but negative, indicating a decrease with elevation (Table 3)

Table 3. Percentage of relative abundance of small mammal species across sites on Mount Meru. A linear regression model (R^2) was used to check the relationship between the percentage of relative abundance of each species and elevation.

Small Mammal Species	SA	LMF	UMF	UMF/EH	EH	AA	Total (R^2)
Rhabdomys dilectus	2.3	1.1	3.4	29.5	22.7	**40.9**	11.0(88) ††
Praomys taitae	0.0	22.4	**59.8**	12.1	5.6	0.0	40.0(321)
Montemys delectorum	0.0	0.0	**66.7**	33.3	0.0	0.0	0.4(3)
Mus triton	0.0	0.0	0.0	0.0	0.0	**100.0**	0.5(4)
Mastomys natalensis	**100.0**	0.0	0.0	0.0	0.0	0.0	3.6(29)
Lophuromys verhageni	0.0	0.0	0.0	22.2	**68.5**	9.3	6.7(54)
Lemniscomys striatus	0.0	0.0	**75.0**	25.0	0.0	0.0	0.5(4)
Graphiurus murinus	0.0	0.0	0.0	**80.8**	19.2	0.0	3.2(26)
Grammomys dolichurus	**28.6**	14.3	23.8	19.0	14.3	0.0	2.6(21)
Dendromus insignis	0.0	0.0	0.0	0.0	**57.1**	42.9	0.9(7) ††
Dasymys incomtus	0.0	**42.9**	42.9	14.3	0.0	0.0	0.9(7)
Cricetomys ansorgei	0.0	**44.4**	33.3	22.2	¥	¥	1.1(9) ¥
Arvicanthis niloticus	**77.3**	22.7	0.0	0.0	0.0	0.0	2.7(22) ††
Crocidura newmarki	1.6	29.9	15.0	18.1	**33.1**	2.4	15.8(127)
Crocidura allex	0.0	0.0	**40.7**	23.5	35.8	0.0	10.1(81)

†† $p < 0.05$; Bold indicates highest percentage of relative abundance of the species between sites. ¥ not determined. SA (savanna); LMF (lower montane forest); UMF (upper montane forest); UMF/EH (upper montane forest/Ericaceous heathland); EH (ericaceous heathland); and AA (Afroalpine).

The Shannon–Wiener index of diversity was highest in the UMF/EH (H′ = 1.94), and lowest in the UMF (H′ = 0.90), as shown in Figure 3A. Values for evenness, also, varied across elevations, with a relatively higher value at the EH (E = 0.75). Figure 3B depicts that there is a tendency for total small–mammals–species and rodent–species richness to be greatest at the UMF/EH and decline substantially at the highest elevations. Likewise, total percentage contribution and percentage of trap success were higher at the UMF and lower in the SA and AA sites (Figure 4). Except for the UMF/EH sites (Figure 5), where *Lemniscomys striatus* was collected on the fourth day, the total number of species reported at each elevation had achieved an asymptote by the third day of trapping. The estimated number of species (Sest) was equal to the observed number of species (Sobs) at all sites, except at the UMF/EH, where it was slightly greater (11.5 species, SE ± 1.10). The total number of species in the overall survey pool was estimated to be 16.2 (SE ± 0.18).

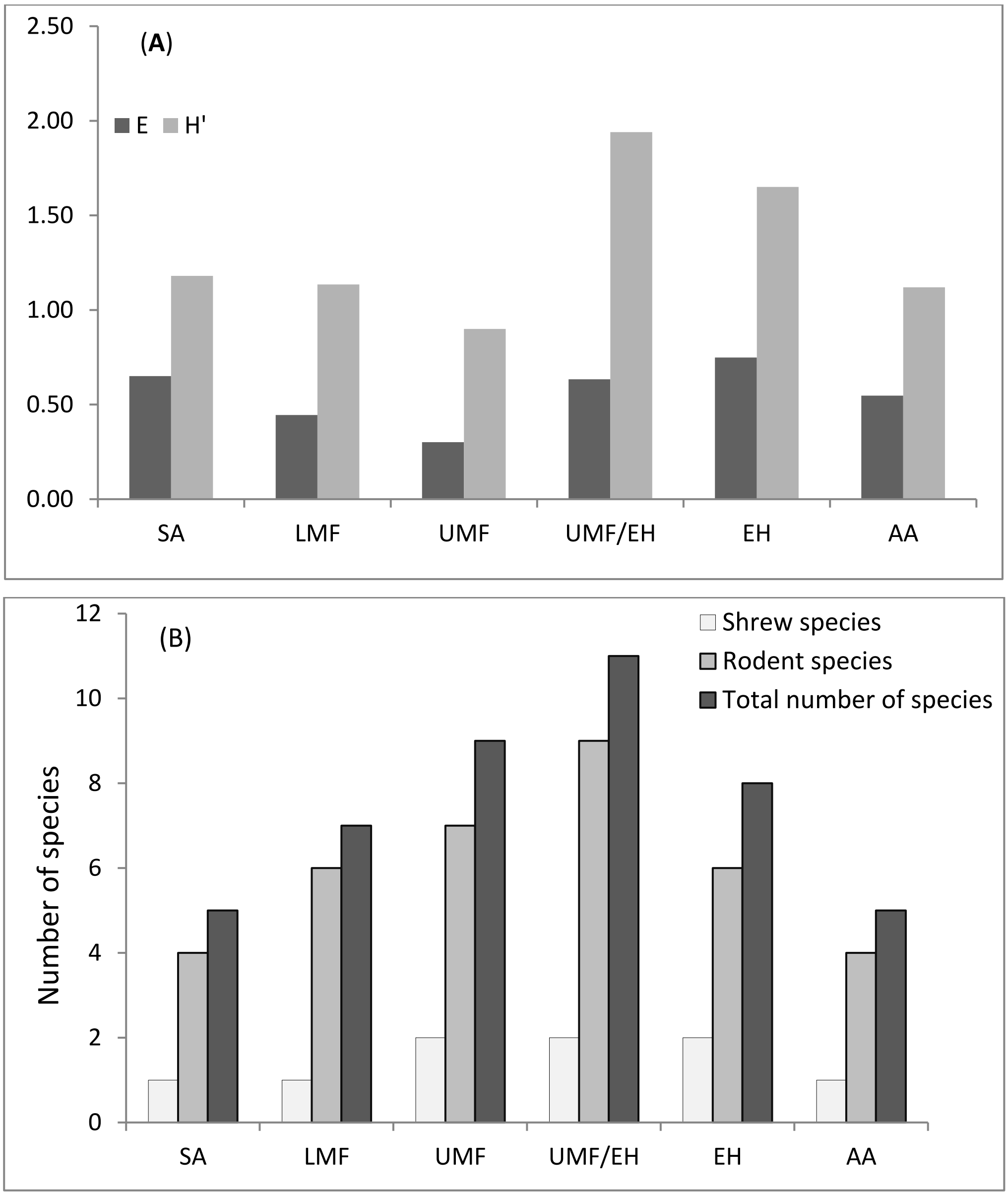

Figure 3. Diversity of small mammals across sites. (**A**) Species diversity evaluated with Shannon diversity index (H′) and evenness (E), and (**B**) species richness.

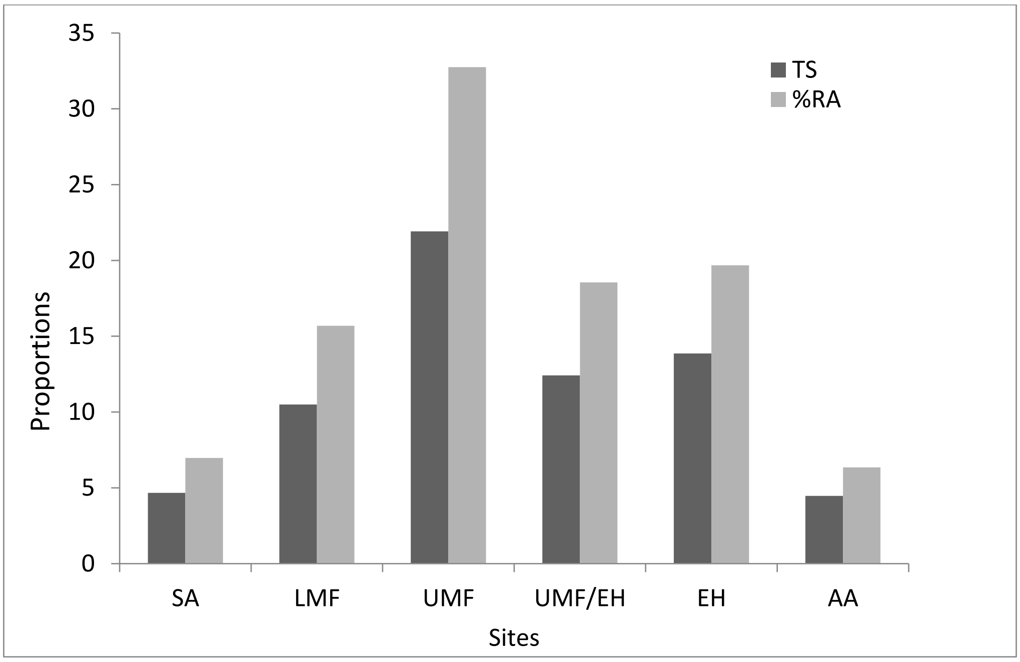

Figure 4. Small mammals's percentage of relative abundance (%RA) and percentage of trap success (TS) across sites.

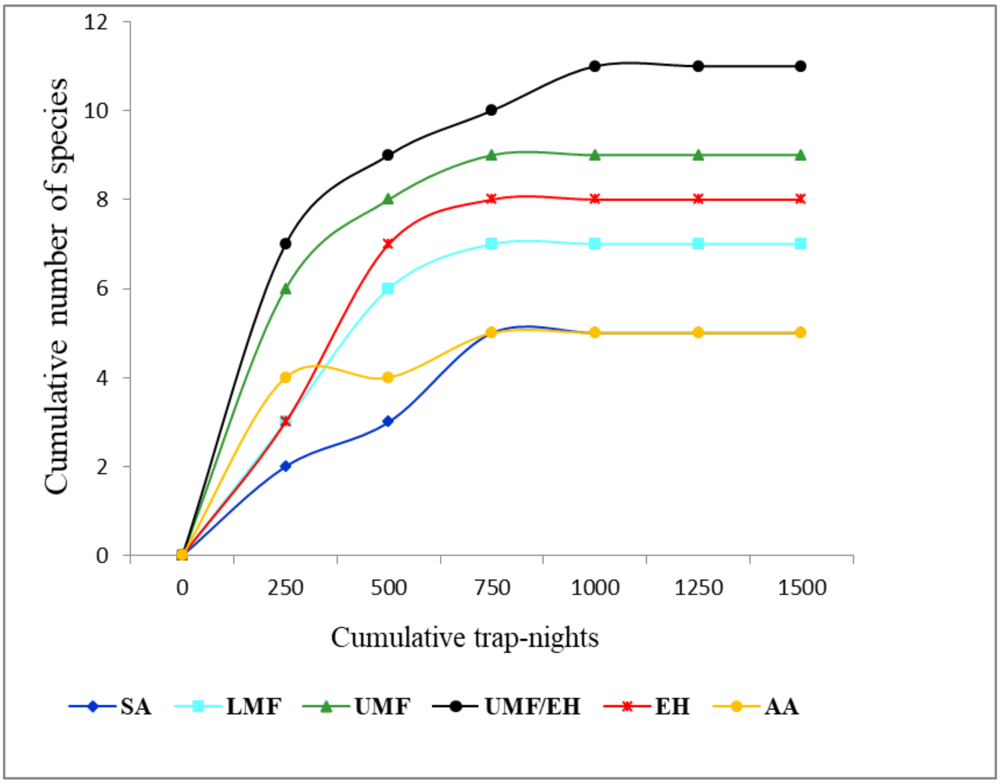

Figure 5. Species accumulation curves for elevations surveyed. The AS and AA sites had the same number of cumulative species starting from the third day of trapping. Asymptote reached on all sites. Trapping effort experssed as trap-nights. SA (savanna); LMF (lower montane forest); UMF (upper montane forest); UMF/EH (upper montane forest/Ericaceous heathland); EH (ericaceous heathland); and AA (Afroalpine).

3.2. Changes in Community Composition in the Last Decade, between 2009 and 2021

We compared small mammal species composition in 2021 against species composition recorded in 2009 (Table 4). Except for the SA, which was sampled only in 2021, both surveys sampled the LMF, UMF, UMF/EH, EH, and AA. The 2009 dataset included 751 small mammal captures (475 rodents and 276 shrews) in 7111 trap nights, with trap success ranging from 3.5% to 18.0% [26]. The rodents and shrews were represented by eight and two species, respectively. The total small mammal species richness in the study area was higher in our survey (15 species) than in 2009 (10 species). *Praomys taitae* was the most abundant species, accounting for 40.7% of total small mammal captures in 2009. The trap success of 2021 was slightly higher than 2009, in most of the sites (Figure 6). The highest percentage of trap success in the 2009 (18.0%) and 2021 (21.9%) surveys was recorded in the UMF zone.

Table 4. Occurrence data in terms of percentage of relative abundance for each species, by elevation zone, in 2009 (numerator) and 2021 (denominator) on Mount Meru.

Species	SA ^{ns}	LMF	UMF	UMF/EH	EH	AA
Rhabdomys dilectus	–/3.6	–/0.8	–/1.1	19.7/17.4	4.5/12.7	48/70.6
Otomys tropicali	–/0.0	–/–	–/–	1.6/–	0.6/–	2.0/–
Praomys taitae ^{D}	–/0.0	47.3/57.1	72.0/73.0	31.1/26.2	2.6/11.4	–/–
Montemys delectorum	–/0.0	–/–	–/0.8	–/0.7	–/–	–/–
Mus triton	–/0.0	–/–	–/–	–/–	0.6/–	–/7.8
Mastomys natalensis ^{d}	–/51.8	–/–	–/–	–/–	–/–	–/–
Lophuromys verhageni	–/0.0	–/–	7.0/–	7.4/8.1	19.4/23.4	4.1/9.8
Lemniscomys striatus ^{D}	–/0.0	–/–	–/1.1	–/0.7	–/–	–/–
Graphiurus murinus ^{D}	–/0.0	3.0/–	0.4/–	4.9/14.1	9.7/3.2	–/–
Grammomys dolichurus ^{D}	–/10.7	1.8/2.4	1.6/1.9	1.6//2.7	2.6/1.9	–/–
Dendromus insignis	–/0.0	–/–	–/–	0.8/–	4.5/2.5	4/5.9
Dasymys incomtus	–/0.0	–/2.4	–/1.1	–/0.7	–/–	–/–
Cricetomys ansorgei	–/0.0	–/3.2	–/1.1	–/1.3	–/–	–/–
Arvicanthis niloticus	–/30.4	–/4.0	–/–	–/–	–/–	–/–
Crocidura newmarki	–/3.6	29.3/30.2	7.0/7.2	18.0/15.4	32.9/26.6	8.0/5.9
Crocidura allex ^{D}	–/0.0	18.6/–	12.1/12.5	14.8/12.8	23.2/18.4	32.0/–
Percentage of contribution per site	–/7.0	22.2/15.7	34.2/32.8	16.2/18.6	20.6/19.7	6.7/6.4
Total number of species	–/5	5/7	6/9	9/11	10/8	6/5
Total number of captures	–/56	167/126	257/263	122/149	156/158	49/51
Trap effort	–/1200	1426/1200	1426/1200	1426/1200	1426/1140	1407/1140
Trap success (%)	–/4.7	11.7/10.5	18.0/21.9	8.6/12.4	10.9/13.9	3.5/4.5

"–" Not recorded. ^{ns} Site not surveyed in 2009, results from 2021 are given for context. ^{D} Species recorded by Demeter and Hutterer [25] within the elevational range of our study. ^{d} Species recorded by Demeter and Hutterer [25] below the elevational range of our study. The faunal lists of Demeter and Hutterer [25] are detailed in Stanley and Kihaule [26]. LMF (lower montane forest); UMF (upper montane forest); UMF/EH (upper montane forest/Ericaceous heathland); EH (ericaceous heathland); and AA (Afroalpine).

Except for *Otomys tropicalis*, there were no small mammal species recorded in 2009 that were not found in our survey. On the contrary, we collected a total of six rodent species (*Arvicanthis niloticus*, *Mastomys natalensis*, *Lemniscomys striatus*, *Dasymys incomtus*, *Cricetomys ansorgei*, and *Montemys delectorum)*, which were not reported in the 2009 survey. Of these, *Mastomys natalensis* was recorded exclusively in the SA, whereas *Arvicanthis niloticus* was recorded in the SA and the LMF zones. *Montemys delectorum*, *Dasymys incomtus*, *Lemniscomys striatus*, and *Cricetomys ansorgei* species were distributed between the LMF and UMF/EH zones.

In total, 9 out of the 16 small mammal species recorded (*Rhabdomys dilectus, Praomys taitae, Mus triton, Lophuromys verhageni, Graphiurus murinus, Grammomys dolichurus, Dendromus insignis, Crocidura newmarki and Crocidura allex*) were documented in both surveys. Of the nine species present in both studies, five species (*Graphiurus murinus, Lophuromys verha-*

geni, Crocidura allex, Dendromus insignis, and *Mus triton*) were recorded at higher elevation zones in 2021 than they were in 2009 (Table 4). The 2009 survey collected *Crocidura allex* across all elevational zones sampled, but they were missing in the LMF and AA zones in our survey. *Graphiurus murinus* was captured from the lowest elevational zones, the LMF (3%; $n = 5$) and UMF (4%; $n = 1$), in the 2009 survey, but we captured *Graphiurus murinus* at higher altitudes in the UMF/EH (4.9%; $n = 1$) and the EH (9.7%; $n = 5$). Similarly, in the 2009 survey, *Lophuromys verhageni* was recorded between the UMF and AA zones, along the elevational gradients, but we began collecting *Lophuromys verhageni* in the UMF/EH (8.1%; $n = 12$). *Dendromus insignis* was collected in the UMF/EH, EH, and AA, whereas our survey started recording at the EH (2.5%; $n = 4$). A single specimen of *Mus triton* was collected from the EH (2.0%; $n = 1$) in 2009, whereas all individuals (7.8%; $n = 4$) in our survey were from the AA zone.

No species recorded at higher elevation zones in 2009 than in 2021. The degree and direction of community compositional changes between the 2009 and 2021 surveys are portrayed with an arrow in Figure 8. The length of the arrows indicates the degree of observed changes in species composition over time. Closer points show a higher degree of similarity in species makeup. Thus, our results revealed that the greater observed changes in species composition occurred in the LMF and UMF. According to PCoA on the Bray–Curtis dissimilarity matrix (Figure 8), 74% of the difference in community dissimilarity is explained by the first two axes. The elevational distribution of species was largely (51%) explained by the first axis of species composition, with the species composition of sites at higher elevations having higher values along Axis 1. Based on correlation analysis, the elevation of sites was positively correlated with the values of Axis 1 (Pearson's $r = 0.93$, $p < 0.001$). Using a paired t–test of Axis 1 values, to compare the 2009 and 2021 community makeup, we found that the 2021 species composition had more negative values in all elevation sites than the 2009 community composition ($t = -3.74$, $p = 0.020$). Hence, over time, the species composition has changed in the negative direction along the first main axis. This indicates that the species composition at higher elevations in 2021 resembles the species composition at lower elevations in 2009.

Meteorological data from Mount Meru showed a trend in increasing temperatures since 1979 (Figure 7). Between 2009 and 2021, it showed a significant increase in mean temperature by 0.37 °C ($p < 0.05$, SE = 0. 20). Increases in temperature are, also, evident in the neighbouring region of Mount Kilimanjaro, with an increase of 0.27 °C per decade [36], although the extent of change varies from one area to another.

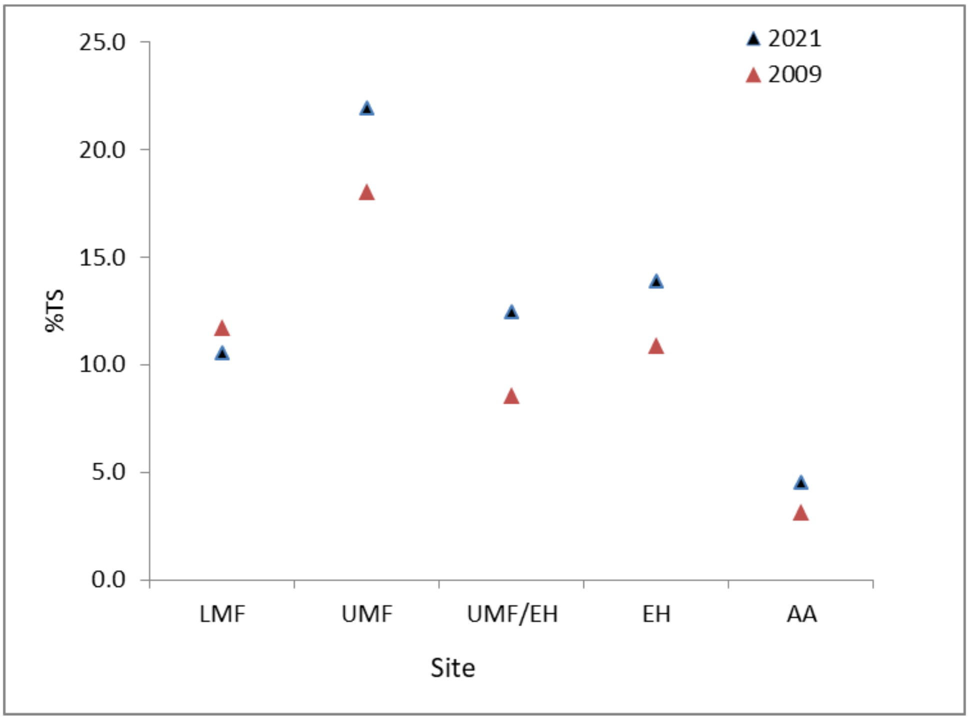

Figure 6. Percentage of trap success (%TS) between the two studies, across sites. LMF (lower montane forest); UMF (upper montane forest); UMF/EH (upper montane forest/Ericaceous heathland); EH (ericaceous heathland); and AA (Afroalpine).

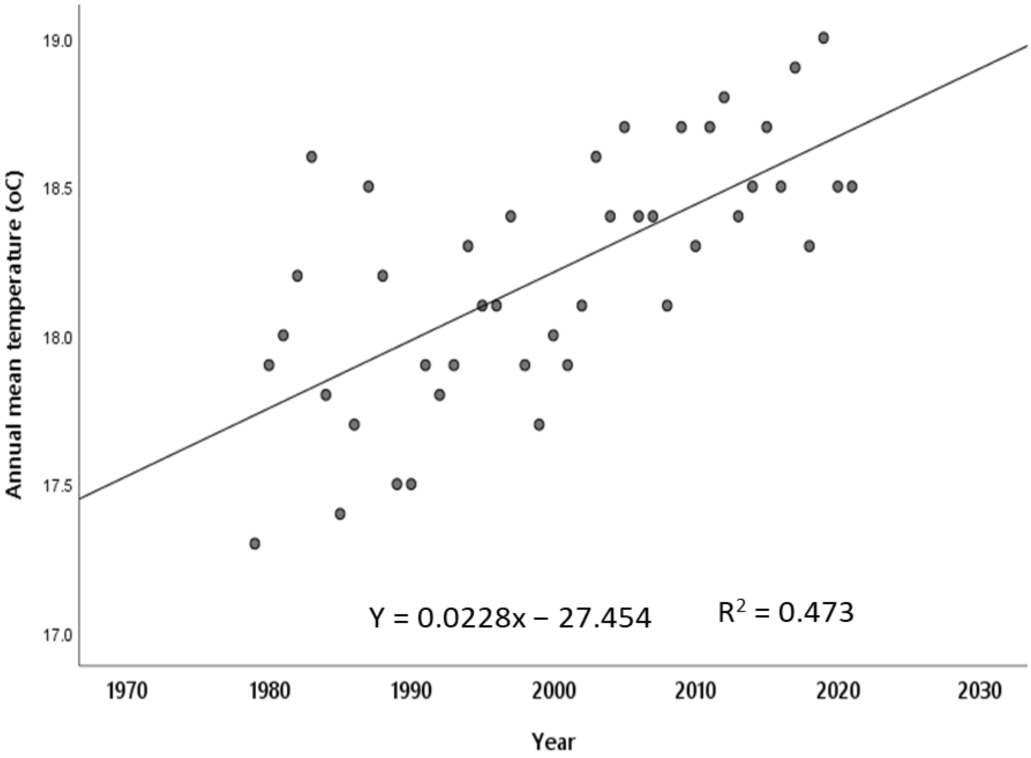

Figure 7. Annual mean temperature changes for Mount Meru, from 1979 to 2021. Linear regression with response variable (Y) and coefficient of determination (R^2).

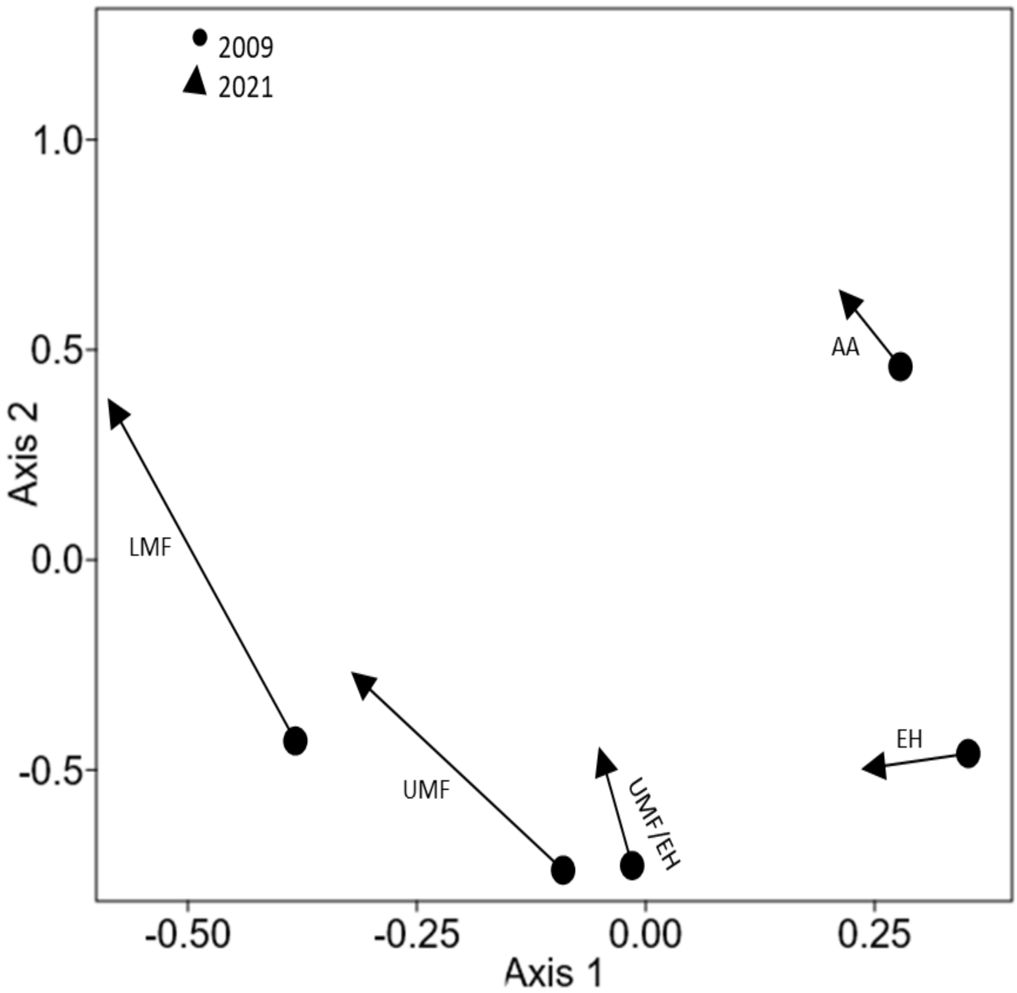

Figure 8. Elevational shifts in the community composition of small mammals on Mount Meru. Arrows indicate the degree of change in species composition between 2009 and 2021, based on the PCoA matrix. Axis 1 and Axis 2 refers to the PCoA 1 and PCoA 2 axis respectively. LMF (lower montane forest); UMF (upper montane forest); UMF/EH (upper montane forest/Ericaceous heathland); EH (ericaceous heathland); and AA (Afroalpine).

4. Discussion

4.1. Diversity and Distribution Patterns

The distribution of small mammals in the current study, generally, varied with elevation zones. We found the highest abundance and relatively lower evenness in the UMF, where *Praomys taitae* predominated. *Praomys taitae* was the most abundant species in our study and was highly confined to forest habitats. According to a previous study, *Praomys* is a forest-dwelling genus [37,38]. Previous studies from this study area [26] and others from Mount Kilimanjaro [17] have, also, reported a high abundance of *Praomys taitae* in the mountain forest habitats. The highest elevational site (AA) contributed the least number of individuals and species richness compared to other habitats. During our trapping in the AA, individuals that died in traps were frequently observed. Low temperatures and other harsh environmental factors affect the abundance of the species found at higher altitudinal levels [13]. At this highest elevation site, we recorded a daily minimum temperature as low as 2.3 °C (Appendix A Table A2). Thus, unfavourable weather conditions, presumably, contributed to the lower number of captures at high altitudes on Mount Meru. Our results support previous studies, showing that high altitudinal zones have comparatively lower species diversity and abundance [16,18].

Rhabdomys dilectus was the second most abundant rodent species in the study area, and was found at all sites, but in high numbers in the UMF/EH and above. Stanley et al. [17] and Stanley and Kihaule [26] reported a higher abundance of *Rhabdomys dilectus* from higher altitudes on Mount Kilimanjaro and Mount Meru, respectively. *Lophuromys verghani*, an endemic species to Mount Meru, is found in the UMF/EH and above. *Lophuromys flavopunctatus*, in the same genus, has been reported to inhabit less favourable habitats at higher altitudes, including ericaceous heath and montane moorlands on Mount Elgon [19]. *Grammomys dolichurus* was captured in all sites, except the Afroalpine zone. Taylor [39] noted that *Grammomys dolichurus* is less specialised in its habitat requirements. *Mastomys natalensis* was restricted to lower–altitude savannas, whereas *Arvicanthis niloticus* was also, abundantly found in the savanna grassland, with a few individuals found in the LMF. The presence of these species in these sites was expected, given that several studies have confirmed their existence at lower elevations, with bushes or tall grasses [40,41]. Stanley [42], also, found a much greater abundance of *Mastomys natalensis*, at elevations below 900 m in the Udzungwa Scarp Forest Reserve. *Crocidura newmarki* was the most widespread endemic shrew species recorded in all vegetation zones, along the elevational gradients. Stanley and Kihaule [26] reported similar habitat occurrence of this species in this study area.

Our results suggest that the sampling effort used was appropriate for documenting small mammal species at different elevations on Mount Meru. By the third day of trapping, the total number of species reported had attained an asymptote at all elevations, except the UMF/EH (*Lemniscomys striatus* collected by the fourth day). Similarly, the estimated (Sest) and observed (Sobs) number of species was similar at almost every site, indicating a limited likelihood of capturing further new species. Thus, it would be tempting to consider that our sampling regime captured a reasonably comprehensive inventory of small mammal species in as few as four trapping days. Our studies may confirm the interpretations of Stanley and Kihaule [43], who recommended additional sampling effort to capture the complete lists of small mammals, since their species accumulation curves failed to achieve a plateau at every site in the study area. In fact, we documented six species that had not previously been recorded.

Unlike in the Udzungwa Mountains and Bwindi National Park, elevation was not significantly correlated with small mammal abundances and species diversity on Mount Meru. In the Udzungwa Mountains, the overall capture of small mammals and species richness of rodents was found to increase with an increase in elevation [21]. In Bwindi National Park, species richness decreased with elevation [44]. No effect of elevation on species richness or abundance was seen in our study, consistent with the report by Stanley and Kihaule [26]. However, it is important to note that, unlike the previous research, our study did not utilise additional pitfall buckets; hence, diversity indices and elevational data were generated for Sherman and Havahart. Our results showed a strong distribution pattern in species richness and abundance of small mammals, with an increase at the intermediate levels and a decrease towards the upper and lower altitudes. Thus, our findings support the hump–shaped distribution hypothesis, which has been observed for non–volant small mammals, across a wide range of altitudinal gradients worldwide [6,9]. We found species diversity to, distinctly, peak in the UMF/EH, a transition zone between upper montane forest and ericaceous heath. The occurrence of a great number of species in this zone provides more evidence for the hypothesis, that the highest species richness at a given altitude is the consequence of overlapping species range with different habitat requirements. On Mount Meru, we can observe this pattern, where vegetation heterogeneity increases and conditions are not too extreme [45,46].

4.2. Possible Changes in Species Composition between 2009 and 2021

Our findings provide evidence that along an elevational gradient on Mount Meru, small mammal species may have shifted their ranges upslope over the last 12 years, resulting in changes in species composition. Since all the species were captured at the highest elevation zone from which they were recorded in 2009, there was no evidence of downslope range shifts. Our analyses indicate that five out of nine species (55.6%) showed upward movement in their elevational range since 2009. This is smaller than that observed in Simien Mountains National Parks [9], where two–thirds (66.6%) of small mammal species have been observed to shift their elevational ranges upslope. The current increasing trend in temperature in Mount Meru may be having an ecological effect on the different habitat types along the elevation gradient and may be driving the observed shift in small mammal community patterns. Rising mean temperature, due to global warming, is predicted to shift various habitat types and ecosystems to higher latitudes and altitudes [8,47]. Since most small mammals are habitat specialists, the shift observed in our study is, most likely, a response to the 0.37 °C increase in the study region's mean average temperature, between the 2009 and 2021 surveys. Nevertheless, when we compare our findings with the 2009 results, there are other factors that should be taken into account, as follows.

First, although most of the sampling area falls within the protected Arusha National Park, human activities such as grazing and deforestation have intensified habitat degradation at the lower altitudes [23]. According to reports, about 60% of mountainous regions are exposed to intensive human pressure, mainly at lower elevations and mountain bases [48]. Therefore, we speculate that human activities may have, also, contributed to the upward elevational shifts in our study area.

Second, our survey used standard Sherman and Havahart traps, while the 2009 survey utilised Museum Special traps, Victor Rat traps, and additional pitfall buckets, to collect some species with low body weight. For example, the lower number of captured individuals for shrews in our survey, compared to 2009, could be related to an underestimation of their ability to be trapped by Sherman traps, due to their small size. As the trappability of species to bait varies, it would be important, also, to note the variations in the types of bait used in both surveys. In addition, considering the inconsistency in trapping seasons in the AA site between the two surveys would also be important, when comparing the 2009 and 2021 findings.

Finally, we expected that lower elevation zones (1700–2300 m) would experience a decrease in species richness over time. It is widely predicted that communities will shift upslope due to climate–related changes, and species richness will decline at lower elevations [3,49]. However, we found a greater number of small mammal species at low elevations over time. The higher species richness in our survey compared to 2009 could be due to two reasons. (i) The sufficiency of our sampling and the types of traps we used. For instance, the presence of *Cricetomys ansorgei* in our survey but not in 2009 is credited to the employment of Havahart traps in our trapping methods, to collect taxa with large body mass. (ii) We, clearly, do not have evidence of the occurrence of the six new species in the SA zone (1500–1700 m), which lies below the elevational range of the 2009 study. However, species that moved upslope from the montane forest zones were, likely, replaced by species from the SA zones, which are savanna habitats. This suggests that the community is shifting upslope due to lowland biotic attrition [50], whereby low and mid–elevation forests gain species from lower elevations. For example, *Arvicanthis niloticus* was not recorded in the 2009 survey, but we found it in the SA and LMF. In addition, Demeter and Hutterer [25] documented *Lemniscomys striatus* and *Graphiurus murinus* in lower elevations, including savanna habitats, whereas in our survey they were, instead, recorded at higher elevation zones, probably confirming that species have moved upward from savanna habitats to montane forest zones. This is supported by previous reports that upslope range shifts, due to climate change on tropical mountainsides, may be compensated by the influx of species currently found at lower elevations or by expansion from small nuclei left over from previous warming episodes [50].

Of the 10 small mammal taxa listed in 2009, *Otomys tropicalis* was not captured in 2021. In 2009, *Otomys tropicalis* was captured in the UMF/EH, EH, and AA elevational zones, which correspond to 2950 m, 3500 m, and 3650 m sites, respectively, in our study. It is very unlikely that their occurrence was underestimated by our sampling methods, since we included the elevation range surveyed in 2009, and our species accumulation curve indicated low probability of capturing new species with more sampling. Hence, this species may be absent or very rare. In addition, Demeter and Hutterer [25] recorded five specimens of *Otomys irroratus*, which was not recorded in 2021. It is widely understood that montane species are expected to experience further upward range shifts in the future, in response to recent temperature increases [51], and species that occur in low densities in narrow habitat bands are the most vulnerable [49,52]. In this manner, the *Otomys tropicalis* in our study area may become endangered, unless they are able to adapt quickly to changing conditions. Unlike lower elevation species, there is nowhere for higher elevation species to go [50,53]. In other words, a species cannot move upward beyond the top of a mountain [52]. Another important point to note here is that the EH belts had experienced a firebreak in 2015 [54]. It is, therefore, worth highlighting that rising temperatures over the past decade and vegetation changes, as a result of fire experience, may have resulted in the local extirpation of *Otomys* species on Mount Meru. However, the fact that our survey used only standard Sherman traps, while the 2009 survey employed different trap types, should not, also, be ruled out in light of the species's absence from record, as some reports mention that *Otomys* species are not easily trapped [55]. Therefore, further research is required to confirm the occurrence status of this species in the study area.

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Institutional Review Board Statement: The ethical clearance for the study was issued by the Tanzania Wildlife Research Institute and COSTECH (2021–008–NA–2020–238). This study was approved by Sokoine University of Agriculture (SUA/ADM/R.1/8/651 and SUA/PFC/D/2019/0021/05) for the use of animals in this study. The permission to work in the study area was sought from the Tanzania National Park Authority (AB.161/376/01).

Data Availability Statement: The data presented in this study are included with in this paper.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Individual captured small mammal species and sampling efforts in the 2009 and 2021 studies on Mount Meru.

Small Mammal Species	SA ns	LMF		UMF		UMF/EH		EH		AA		TOTAL	
	2021	2009	2021	2009	2021	2009	2021	2009	2021	2009	2021	2009	2021
Rhabdomys dilectus	2	0	1	0	3	24	26	7	20	24	36	55	88
Otomys tropicali	0	0	72	0	192	2	39	1	18	1	0	4	321
Praomys taitae	0	79	0	185	0	38	0	4	0	0	0	306	0
Montemys delectorum @	0	0	0	0	2	0	1	0	0	0	0	0	3
Mus triton	0	0	0	0	0	0	0	0	0	1	4	1	4
Mastomys natalensis	29	0	0	0	0	0	0	0	0	0	0	0	29
Lophuromys verhageni	0	0	0	18	0	9	12	30	37	2	5	59	54
Lemniscomys striatus	0	0	0	0	3	0	1	0	0	0	0	0	4
Graphiurus murinus	0	5	0	1	0	6	21	15	5	0	0	27	26
Grammomys dolichurus	6	3	3	4	5	2	4	4	3	0	0	13	21
Dendromus insignis	0	0	0	0	0	1	0	7	4	2	3	10	7
Dasymys incomtus	0	0	3	0	3	0	1	0	0	0	0	0	7
Cricetomys ansorgei	0	0	4	0	3	0	2	0	–	0	–	0	9
Arvicanthis niloticus	17	0	5	0	0	0	0	0	0	0	0	0	22
Crocidura newmarki	2	49	38	18	19	22	23	51	42	4	3	144	127
Crocidura allex	0	31	0	31	33	18	19	36	29	16	0	132	81
Species richness	5	5	7	6	9	9	11	10	8	6	5	10	15
Total number of captures	56	167	126	257	263	122	149	155	158	50	51	751	803
Total trap-effort	1200	1426	1200	1426	1200	1426	1200	1426	1140	1407	1140	7111	7080
Trap success	4.7	11.7	10.5	18	21.9	8.6	12.4	10.9	13.8	3.5	4.5	10.5	11.3

@ *As Praomys delectorum* in previous studies (but see Nicolas et al., 2021); ns Not sampled in 2009.

Table A2. Climate data registered at each elevational site on Mount Meru in February–November 2021 during the small mammal survey. Totals presented as mean and standard deviation (Mean ± SD), range(R) and number of days measured (N). The rainfall samples are expressed as the number of days measured and number of days with rain (in parenthesis).

Elevation Zone	Daily Rainfall (mm)	Daily Minimum Temperature (°C)	Daily Maximum Temperature (°C)
SA			
Mean ± SD	0.1 ± 0.3	20.6 ± 5.8	20.9 ± 5.8
R	0–0.7	12.5–28.1	12.6–28.3
N	6(1)	6	6
LMF			
Mean ± SD	0	14.5 ± 1.5	15.6 ± 1.8
R	0	11.6–15.7	12.3–17.5
N	6(0)	6	6
UMF			
Mean ± SD	2.5 ± 1.4	14.7 ± 2.2	15.4 ± 2.8
R	0–4.1	13.3–18.9	13.6 ± 19.1
N	6(2)	6	6
UMF/EH			
Mean ± SD	2.2 ± 1.7	10 ± 0.34	12.5 ± 2.0
R	0–3.8	9.5–10.5	10.4–15.9
N	5(4)	5	5
EH			
Mean ± SD	3.3 ± 1.6	10.3 ± 0.2	12.8 ± 2.2
R	0–4.2	10.1–10.5	10.6–16.4
N	6(2)	6	6
AA			

Table A2. *Cont.*

Elevation Zone	Daily Rainfall (mm)	Daily Minimum Temperature (°C)	Daily Maximum Temperature (°C)
Mean ± SD	1.7 ± 1.9	5.5 ± 2.4	8 ± 1.3
R	0–3.8	2.3 ± 8.3	6.9–10.3
N	5(3)	5	5

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