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Ant Diversity Declines with Increasing Elevation along the Udzungwa Mountains, Tanzania

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Abstract: Biodiversity patterns along elevational gradients are generally characterised by monotonic decreases or mid-elevational peaks in species richness, while elevational zones may be characterised by distinct assemblages, or higher zones may be subsets of lowland assemblages. Elevational gradients in diversity have been less studied in the Afrotropical region. This study documents ant diversity patterns in three forest types associated with the tropical mountains of Udzungwa; we hypothesise that: (1) ant diversity and activity will show a monotonic decrease from mid-elevation with increasing elevation and (2) that forests associated with different elevations will have a distinct ant assemblage. Pitfall traps were deployed at three targeted elevations (650–800, 800–1400, and 1400–1500 m a.s.l.). Ant species richness declined with increasing elevation from 650 m a.s.l. and formed three elevational assemblages with lower elevation forests having almost twice as many species as sub-montane forests and three times as many as that of the montane forests. In contrast, overall ant activity peaked at 800–1400 m a.s.l. The ant assemblages associated with the lower elevation forest were very distinct, while assemblages associated with the sub-montane and montane forests shared species. Our study reveals valuable and relevant information for biodiversity monitoring and conservation planning as the species associated with each forest type may be used as indicator species for assessing biodiversity responses to climate change and anthropogenic activities on these mountains.

Keywords: ant assemblages; elevational gradients; biodiversity; ants (Hymenoptera, Formicidae); Eastern Arc Mountains

Citation: Kunene, C.; Foord, S.H.; Scharff, N.; Pape, T.; Malumbres-Olarte, J.; Munyai, T.C. Ant Diversity Declines with Increasing Elevation along the Udzungwa Mountains, Tanzania. *Diversity* **2022**, *14*, 260. https://doi.org/10.3390/d14040260

Academic Editor: Alan N. Andersen

Received: 7 January 2022
Accepted: 26 March 2022
Published: 30 March 2022

1. Introduction

One of the central goals in ecology is to understand distributional patterns and the abundance of living organisms. This understanding allows ecologists to assess and monitor changes in ecosystems and develop conservation priorities and policies [1,2]. To achieve this goal, ecologists must first quantify and characterise communities across various ecosystems. This involves a description of assemblage structures and their variations across time and space [3].

Environmental gradients have been the target of much research; they facilitate studying the response of biodiversity to climatic conditions and how they vary across space and time [4–10]. The latitudinal gradient of increasing richness from polar regions to the equator [7] has been one of the best documented biodiversity patterns and is relatively consistent across taxa and regions [11]. Elevational gradients have also been widely studied, but changes in biodiversity along this gradient vary depending on the taxa as well as region [12–14].

Altitudinal gradients are powerful model systems [15]. They provide natural experiments for investigating the response of biodiversity to environmental conditions within a small geographic space [16], which makes it particularly easy to test hypotheses about patterns and processes that may occur at a larger scale [17]. The drop in air temperature by 0.6–1.0 °C for every 100 m rise in elevation limits species from moving further up the mountain (especially thermophilic species) and suggests that ecosystems at high altitudes (with the predicted 2 °C increase in air temperature by year 2100) are more vulnerable to climate change, making research on patterns along altitudinal gradients important for conservation [18,19]. Climate change research [20–22] predicts a general increase in annual average temperature globally, which will shift eco-zones upwards and result in the disappearance of habitats. This may result in the extinction of affected species and negatively impact local ecosystem functioning [23]. Therefore, it is important to map and understand biodiversity patterns and identify the factors that generate and sustain high concentrations of biodiversity along elevations to support conservation programmes.

The Udzungwa Mountains are part of the Eastern Arc Mountains, a mountain chain stretching from Southeastern Kenya to Southern Tanzania along the coast [24,25]. This mountain chain, together with other Afromontane areas in Eastern Zaire and Ethiopia, is recognised as a biodiversity hotspot [26] and a conservation site for iconic endemic primate species, such as the Udzungwa red colobus (*Piliocolobus gordonorum* Matschie, 1900) and the Sanje mangabey (*Cercocebus sanjei* Mittermeier, 1986) [27,28]. Arguably, it also hosts the second richest bird diversity in Africa [27]. Much of what is known about the faunal diversity is from avifauna [27,29,30] and mammal studies [25,31,32], and very little is known about invertebrates, with data emerging especially for slugs [33], spiders [3], millipedes [34], dragonflies [35], Lepidoptera [36], and beetles [37].

Ants are a diverse and important group of insects in tropical rainforests [38]. They contribute an estimated 10–20% of animal biomass in terrestrial ecosystems and are of great ecological importance [39] as they are found in all forest strata and serve as herbivores, scavengers, and predators. Furthermore, they are ecosystem engineers [40] and can be used as biological indicators [41]. The species composition and ecological characteristics of ants species vary along environmental gradients [42], therefore making the presence or absence of a particular species a potentially appropriate indicator of environmental stress [42,43]. Climatic variables, especially temperature and precipitation, are some of the main drivers of ant diversity and assemblage composition across gradients [13,16].

For ant species richness, two general patterns have been observed across elevational gradients: either a decline with increasing elevation [38] or mid-elevational peak [12]. While some studies have reported an increase in ant species richness with increasing elevation, other studies have observed no clear pattern [44]. However, most of these studies set their lowest elevation at 500 m asl, so they assessed only partial gradients.

Here, we document the diversity patterns of ant communities in three forest types along an altitudinal gradient in the Udzungwa Mountains and characterise them by testing the following hypotheses: (1) ant diversity will decline with increasing elevation considering that ants are largely thermophilic, and (2) there will be distinct ant assemblage compositions that correspond to the three main forest types at different elevations.

Our findings will contribute to the knowledge on how Afrotropical ants are distributed along the main forest and in elevation. Furthermore, our findings will reveal useful and relevant information for biodiversity monitoring and conservation planning.

2. Materials and Methods

2.1. Study Site Description

The Udzungwa Mountains (−8.503722 35.9076; −7.678377 36.94129) are widely recognised for their outstanding biodiversity and high endemicity [28]. They form the largest mountain block of the Eastern Arc Mountains [45] covering 10,000 km ^{2}. Their long-term climatic stability has allowed the habitats in these mountains to endure for millions of years [24]. The Udzungwa mountain ranges in altitude from 200 to 2500 m a.s.l. along which different habitats are found, including lower elevation rainforest (300–800 m a.s.l.); sub-montane rainforest (700–1400 m a.s.l.) covered by a moist forest consisting of evergreen species; montane rainforest (1400–1800 m a.s.l.); and mountain bamboo forest (2400 m a.s.l.) covered by a mosaic of bamboo (*Sinarundinaria alpina*) and *Hagenia abyssinica*, as described by Shangali et al. [46]. The climate in the Udzungwa Mountains is variable, and the eastern slopes receive 2000–3000 mm of rain per year due to the influence of the Indian Ocean [25,47]. More specifically, the lower elevation forest experiences an average temperature of 22.9 °C and an average humidity of 88%. The sub-montane and montane forests experience an average temperature of 20.02 °C and 17.08 °C, respectively, while the humidity is 94.26% and 96.25%, respectively. The main rainy season is between March and May, and there is a light rainy season between November and February [47]. Our study was conducted in the Udzungwa Mountain National Park and the Uzungwa Scarp Nature Reserve in the southern part of the Udzungwa Mountains [25].

2.2. Ant Sampling

We set up five elevational transects, each with a 50 m × 50 m square plot at targeted elevations (650–800, 800–1400, and 1400–1500 m a.s.l.) for a total of 15 plots (Figure S1). These three elevations correspond to three main forest types: lower elevation forest, submontane forest, and montane forest, respectively (Table 1) [48]. The five transects were separated horizontally by 0.1, 1, 20, and 175 km from the first transect (Figure S1). At each 50 m × 50 m square plot, 12 pitfall traps were installed 4 m apart on each side of the plot (Figure S1) for a total of 48 traps. However, it needs to be noted that the lowest sampled elevation was 650 m a.s.l.; therefore, we studied a partial gradient.

Table 1. Description of the three studied forest habitat types in the Udzungwa Mountains, Tanzania.

Habitat Types	Altitudinal Range	Description
Lower elevation forest (lowest elevation)	650–800	Forest with deciduous and semi-deciduous trees, canopy 15–25 m with emergents reaching 50 m
Sub-montane forest (mid elevation)	800–1400	Moist forest with mainly evergreen species, canopy 25–40 m with emergents reaching 50 m
Montane forest (high elevation)	1400–2600	Evergreen moist forest, with canopy height progressively lower with increasing altitude

We combined four contiguous traps to form a sample so that we obtained 12 samples from each plot. This sampling design was part of the application of the Conservation Oriented Biodiversity Rapid Assessment for Tropical Forests (COBRA-TF) sampling protocol [49]. Pitfall traps were partly filled with preservative solution (propylene glycol) and a few drops of liquid soap to break the surface tension and to be protected against rain and falling leaves using lids on stilts about 2–3 cm above the ground. The traps ran for 14 days from October to November in 2014.

Samples were washed and sorted in the laboratory and stored in 96% ethanol at −20 °C. Ants were identified to genus using Fisher and Bolton [50] and then identified to species where possible using online databases, viz., AntWiki (http://www.antwiki.org/, accessed on 22 March 2019) and AntWeb (http://antweb.org/, accessed on 25 March 2019). Number codes were assigned to unidentified ant species. Voucher specimens of all species are deposited in the Natural History Museum of Denmark.

2.3. Data Analysis

Sample coverage for species richness was analysed in iNEXT online software [51]. Sampling completeness based on Chao1 richness estimators was determined using EstimateS (Version 9.1.0) [52], and graphs were drawn using R [53]. Chao1 is a known qualitative measure of alpha diversity that considers the ratio of singletons to doubletons and, therefore, considers rare species. The Simpson diversity index was also used to compare dominance between the three main habitats and plots.

The species composition of the ant communities was visualised by non-metric multidimensional scaling (nMDS) using Sorensen's index dissimilarity matrix based on presence/absence data. The comparison of species composition within the three habitat types was conducted using PERMANOVA in R [53]. The characteristic species of each habitat was determined using the Indicator Value Method (IndVal), which uses the degrees of specificity (uniqueness to a particular site) and fidelity (frequency within the vegetation type/aspect) of each species [54]. An indicator value above 70% shows that a species is both highly specific and has a high fidelity to a given site. The significance of the IndVal values was then tested by random reallocation of replicates among groups [44].

3. Results

3.1. Ant Diversity across Three Main Forest Types along the Elevational Gradient

A total of 31 776 ant specimens belonging to five subfamilies, 34 genera, and 101 morphospecies was collected (Table S1). Myrmicinae was the most diverse subfamily with the highest number (54%) of ant foragers in pitfall traps, 50% of the total number of species (51 species), and 41% of the total number of genera (Table 2). The second most diverse subfamily was Ponerinae with 24% of the species and 29% of the total number of genera, followed by Formicinae with 19% of the species and 18% of the total number of genera. The least diverse subfamilies were Dolichoderinae and Dorylinae with 3% and 4% of the total species richness, respectively. However, Dorylinae had the second highest ant activities. The most speciose genera were *Tetramorium* (19 species), *Pheidole* (8 species), and *Strumigenys* (6 species), while *Camponotus* and *Crematogaster* had five species each (Table S1).

Table 2. Number of genera, species richness, and individuals (activities) of ant subfamilies collected in the study.

Subfamily	Species	Individuals (Activities)
Dolichoderinae		
Technomyrmex	3	5
Dorylinae		
Aenictus	1	2
Dorylus	1	13,260
Parasyscia	2	4
Formicinae		
Camponotus	5	68
Lepisiota	5	209
Nylanderia	1	156
Plagiolepis	3	8
Polyrhachis	2	15
Tapinolepsis	3	10
Myrmicinae		
Calyptomyrmex	1	1
Cardiocondyla	1	6
Carebara	2	126
Catalaucus	1	1
Crematogaster	5	50
Melissotarsus	1	1
Meranoplus	1	7

Table 2. *Cont.*

Subfamily	Species	Individuals (Activities)
Microdaceton	1	1
Monomorium	2	49
Myrmicaria	1	10,512
Pheidole	8	4751
Solenopsis	2	308
Strumigenys	6	83
Tetramorium	19	1261
Ponerinae		
Anochectus	3	5
Bothroponera	4	79
Cryptopone	1	1
Hypoponera	4	11
Leptogenys	4	449
Megaponera	1	210
Mesoponera	3	35
Odontomachus	1	10
Plectroctena	3	82

3.2. Sampling Completeness

Sampling coverage was nearly complete for the three habitat types, lower elevation, sub-montane, and montane forests, as sampling coverage was close to 1 (Table 3). Coverage was the lowest in lower elevation forests (Figure S2).

Table 3. Observed number of species (per habitat and plots), Simpson's diversity index, and sample coverage for each sampling plot in the three habitat types (lower elevation, sub-montane, and montane forests).

Habitat Type	Observed Species per Habitat (Mean SD)	Plot	Altitude m a.s.l	Observed Species Richness per Plot	Simpson's Diversity Index	Sample Coverage
Lower elevation	71 (30.6 ± 8.1)	1	650	31	0.500	0.9963
		2	650	38	0.375	0.996
		7	708	40	0.862	0.993
		10	674	22	0.405	0.989
		13	659	24	0.825	0.974
Sub-montane	44 (19.6 ± 5.3)	3	1005	24	0.297	0.998
		4	993	21	0.447	0.995
		8	978	25	0.623	0.998
		11	1006	15	0.666	0.996
		14	908	13	0.813	0.911
Montane	33 (15.2 ± 6.5)	5	1448	23	0.747	0.994
		6	1482	18	0.271	1
		9	1527	15	0.820	0.995
		12	1552	15	0.466	0.986
		15	1531	5	0.261	0.986

3.3. Species Diversity Patterns

Ant activity, which is represented by the total number of individuals per plot, was the highest at mid-elevation mainly because of *Myrmicaria rustica angustior* (27% of the total activities). At low elevations, *Dorylus helvolus* dominated ant activities and contributed 27% of the total ant activities. Simpson's index suggests that lower elevation forest ant communities were the most diverse (0.664), followed by the mid-elevation ones (0.49), with the high elevation communities being the least diverse (0.44). Species richness was higher at low elevations (31 ± 8), followed by mid-elevations (20 ± 9), and finally high elevations

(15 ± 7) (Table 3). In the low elevation forest, seventy-four percent of the species were found, while 44% and 33% were collected in the sub-montane and montane forests, respectively.

3.4. Ant Assemblage Composition across Gradients

The NMDS showed distinct species assemblages according to their elevations (Figure 1; Figure S3). PERMANOVA confirmed significant differences in species composition between plots at the three elevations (df = 2; Pseudo-F = 2.7863; p = 0.002).

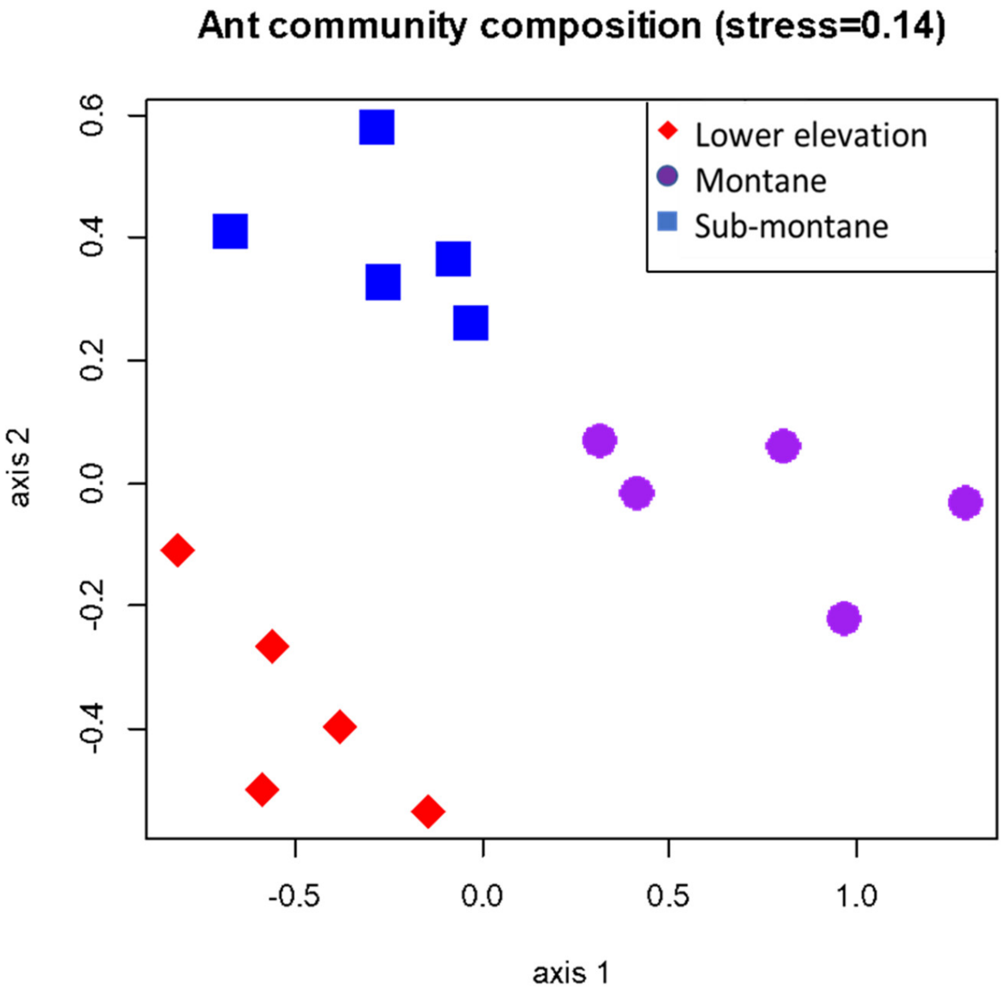

Figure 1. Non-metric multidimensional scaling (NDMS) of community similarity (Bray–Curtis dissimilarity index) based on ant species found in three forests types—lower elevation (red), sub-montane (purple), and montane (blue)—in the Udzungwa Mountains, Tanzania.

3.5. Indicators Species

Fifteen species had a wide distribution and occurred at all elevations; thirty-seven species were associated with the lower elevation forest, eleven were associated with the sub-montane, and nine were associated with the montane forest (Figure S3; Table S1). However, the latter species were not characteristic of the different forest types. Five species were exclusively sampled in the lower elevation forest, while the sub-montane forest and montane forest had two characteristic species each (Table 4).

Table 4. Indicator values (IndVal) of ant species for forest habitat types along the elevational transects. All indicator values are significant ($p < 0.05$).

Habitat Type	Species	Indicator Value (%)
Lower elevation	*Pheidole* sp.05	100
	Megaponera analis rapax	99.52
	Camponotus sp.02. (*etiolipes* gp.)	94.12
	Tetramorium cf. *yarthiellum*	80
	Nylanderia sp.01	70.77
Sub-montane	*Bothroponera* sp.01	85.71
	Myrmicaria rustica angustior	81.23
Montane	*Tetramorium* sp.14	100
	Mesoponera sp.02	82.61

4. Discussion

Ant species numbers declined with increasing elevation from 650 m a.s.l. along the Udzungwa Mountains. This is a widely observed pattern along elevational gradients [55,56] but not for all other taxa studied across the Udzungwa Mountains. Along these mountains, ground dwelling spiders increased with elevation [3], bird richness peaked at mid-elevations [30], and plants and small mammals increased with elevation [24,57]; however, it needs to be noted that all these studies were along a partial gradient. Similarly, in other Afrotropical studies, ant species richness patterns along partial elevation gradients varied between mountains and aspects. A mid-elevation peak was observed along the Maloti-Drakensberg mountains (900 to 3000 m a.s.l.) [16] and northern aspect of Soutpansberg mountains (800 to 1700 m asl) but decreased with elevation on the southern aspect of the latter mountain [13], while a complete gradient by Botes, McGeoch, Robertson, van Niekerk, Davids, and Chown [44] along the Cederberg mountains (sea level—1926 m a.s.l.) reported no clear pattern in their study.

It is widely accepted that ants are generally thermophilic [43]. The distribution of ants is mainly determined by their tolerance to heat [58]; therefore, a decrease in ant species along an altitudinal gradient may be explained by the decrease in temperature with altitude [16,17]. Cooler temperatures may slow down metabolic processes of ants, affect the development of eggs and larvae, affect their foraging activities, and consequently reduce their primary productivity [59]. The limited tolerance of ants to the cold may also cause niche conservatism and limit their species ranges [60]. Mountain areas have bands of climatic conditions that act as barriers, limiting the establishment of species in different areas. Each barrier, therefore, creates a difference in species richness [60,61].

Three highly distinct ant assemblages associated with the three forest types were evident. These findings are similar to those of spiders in the Udzungwa Mountains [3]. However, ant assemblages seem to be more distinct, and lower elevation forests had the most distinct assemblages while montane and sub-montane shared species between them (Figure S3). Tropical species have narrow elevational ranges as the stable local environmental conditions allow them to specialise relative to those specific conditions [62]. The latter may explain the separation of assemblages with respect to elevation zones. The distinct low elevation assemblages may be a result of many tropical lower elevation species possessing narrow fundamental niches limiting their distribution to the lower elevation, while other species may occur in more than one elevation as a result of their wider tolerances [63].

The homogeneous habitat structure, as described by some authors (for example, see Lovett [48]), might be the reason for the similarities between the mid- and high-elevation communities, and therefore resembles the distribution of spider communities on the same mountain [3]. However, other important factors may structure arthropod assemblages that might have contributed to this pattern: for example, how species are specialised to resources and their physiological tolerances to climatic conditions [63].

In the tropics, lowland species are reported to have very narrow fundamental niches, which limits their distribution to the lowland [64], which matches our findings (Figure S2). These species vary from subterranean species, a widely distributed *Technomyrmex pallipes*, to the common rainforest ant *Odontomachus assiniensis*, a predatory species common in evergreen forests as well as the common and generalist ant species *Monomorium mirandum* [65]. Many of the ant species in this study favour the lower elevation forest, as shown by the number of species and species associations.

Fewer ant species were restricted to the montane forest, and only two were characteristic of this forest type. Some species seemed to have larger distributional ranges as they were found in all three vegetation zones. This is typical of tropical species at higher elevations as they tend to be generalists with wider tolerances [66] compared to those in lower elevation forests. However, in the current study, species showing wide tolerances were found across the mountain. Amongst them were both generalists and specialised genera such as *Myrmicaria* (Tropical Climate Specialists), *Pheidole* (Generalised Myrmicinae), and *Solenopsis* (Hot Climate Specialists) [67]. However, all these species may be generalists on these mountains as they have wide geographic distribution and show no habitat preferences.

The two most abundant species were *Myrmicaria rustica angustior* and *Dorylus helvolus*. The former is found in open areas of Afrotropical regions, and together with some other species in the genus *Myrmicaria*, they are well-known honeydew feeders and scavengers [68], while some species are even predatory, feeding on other insects. In the current study, *Myrmicaria rustica angustior* was collected in all habitats and, therefore, did not show any habitat preferences. This can be explained by the fact that the species of genus *Myrmicaria* do not have a specialised diet [69,70]. *Myrmicaria rustica angustior* activity peaked at mid-elevations, perhaps owing to overlapping ranges of the lower elevation and montane forests resulting in the edges providing more open habitats for ants to inhabit [64]. However, another influential species, *Dorylus helvolus,* declined in abundance with increasing elevation. The species of genus *Dorylus* are generalist predators that consume any kind of prey ranging from immatures of other insects to vertebrate carrion, and this may explain their occurrence throughout the mountains [69]. Moreover, the *Dorylus* species are known to move nests in response to prey availability [71] and are most likely to have been influenced by this foraging behaviour as their colonies migrate to new colonies in irregular intervals resulting in new colonies forming through colony fission [69].

5. Conclusions

Conservation plans can benefit from the information that we provide here: The species that we have identified as associated with each forest type may be used as an indicator species for monitoring the response of biodiversity to climate change and anthropogenic activities on these mountains. The importance of the Udzungwa Mountains for conserving Eastern Arc biodiversity has been emphasised [27], but biological data on mainly vertebrates and plants have been used in current conservation strategies. Furthermore, there is an urgent need for further research on the effects of the environmental and climatic factors on the diversity patterns of invertebrate communities in the Eastern Arc Mountains.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/d14040260/s1, Figure S1: The five (50 m $\times$ 50 m) plots consisting of 12 pitfall traps on each side of the plot 4 m apart at each elevation (lower elevation rainforest (650–800 m.a.s.l), sub-montane rainforest (800–1400 m.a.s.l), montane rainforest (1400–1500 m.a.s.l)), Figure S2: Interpolation and extrapolation of species diversity at three forest types (lower elevation, sub-montane, and montane) across the studied communities, Figure S3: A Venn diagram showing the number of species restricted and shared within the three forest types of the Udzungwa mountains and Table S1: Checklist of subfamilies and ant species collected in three habitat types of the Udzungwa mountains.

Author Contributions: J.M.-O., N.S. and T.P. designed the study and collected data; T.C.M. identified the ants; C.K. analysed the data and led the writing of the manuscript under the supervision of T.C.M. and S.H.F.; C.K., S.H.F., T.C.M., J.M.-O., N.S. and T.P. read, edited, and agreed to the published version of the manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: The South African National Research Foundation, grant number 114416 to TC Munyai, grant number 87311 to SH Foord and Danish National Research Foundation for the funding (grant number DNRF96) provided to the Center for Macroecology, Evolution and Climate. NS and TP also acknowledge the support by the Carlsberg Foundation (project 2012_01_0504).

Institutional Review Board Statement: Sampling permits were provided by Tanzania National Parks (TANAPA), the Tanzania Commission for Science and Technology (COSTECH), and the Tanzania Wildlife Research Institute (TAWIRI).

Informed Consent Statement: Not applicable.

Data Availability Statement: The data presented in this study are openly available in FigShare at https://doi.org/10.6084/m9.figshare.19447445.v1.

Acknowledgments: We thank Tanzania National Parks (TANAPA), the Tanzania Commission for Science and Technology (COSTECH), and the Tanzania Wildlife Research Institute (TAWIRI) for providing permits to perform research in the Udzungwa Mountains National Park. Richard M. L. Laizzer and Aloyce Mwakisoma provided invaluable assistance in the field, and the Udzungwa Ecological Monitoring Center (UEMC) and its staff provided logistical support.

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

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