



# The same but different: equally megadiverse but taxonomically variant spider communities along an elevational gradient

Jagoba Malumbres-Olarte<sup>a,b,\*</sup>, Luís Crespo<sup>b</sup>, Pedro Cardoso<sup>c</sup>, Tamás Szűts<sup>d</sup>, Wouter Fannes<sup>e</sup>, Thomas Pape<sup>f</sup>, Nikolaj Scharff<sup>a</sup>

<sup>a</sup> Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark

<sup>b</sup> Biodiversity Research Institute and Department of Evolutionary Biology, Ecology and Environmental Sciences, Universitat de Barcelona, Av. Diagonal 645, 08028 Barcelona, Spain

<sup>c</sup> Finnish Museum of Natural History, University of Helsinki, Helsinki, Finland

<sup>d</sup> Department of Biology, Savaria University Center, Eötvös Lóránd University, Szombathely, Hungary

<sup>e</sup> Department of Biology, Royal Museum for Central Africa, Tervuren, Belgium

<sup>f</sup> Biosystematic Section, Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark

## ARTICLE INFO

### Keywords:

Altitudinal/ elevational gradient  
Climatic stability  
COBRA protocol  
Species richness  
Tropical forest

## ABSTRACT

Spatial variation in biodiversity is one of the key pieces of information for the delimitation and prioritisation of protected areas. This information is especially important when the protected area includes different climatic and habitat conditions and communities, such as those along elevational gradients. Here we test whether the megadiverse communities of spiders along an elevational gradient change according to two diversity models – a monotonic decrease or a hump-shaped pattern in species richness. We also measure compositional variation along and within elevations, and test the role of the preference of microhabitat (vegetation strata) and the functional (guild) structure of species in the changes. We sampled multiple spider communities using standardised and optimised sampling in three forest types, each at a different elevation along a climatic gradient. The elevational transects were at increasing horizontal distances (between 0.1 and 175 km) in the Udzungwa Mountains, Eastern Arc Mountains, Tanzania. The number of species was similar between plots and forest types, and therefore the pattern did not match either diversity model. However, species composition changed significantly with a gradual change along elevations. Although the number of species per microhabitat and guild also remained similar across elevations, the number of individuals varied, e.g. at higher elevations low canopy vegetation was inhabited by more spiders, and the spiders belonging to guilds that typically use this microhabitat were more abundant. Our findings reflect the complex effects of habitat-microhabitat interactions on spider communities at the individual, species and guild levels. If we aim to understand and conserve some of the most diverse communities in the world, researchers and managers may need to place more attention to small scale and microhabitat characteristics upon which communities depend.

## 1. Introduction

Whether one aims at testing the effects of environmental factors, historical events or biotic interactions on biodiversity, or at understanding the scale at which species co-exist or interact, the first step must be to quantify and characterise communities (Basset, 1996; Schaffers et al., 2008; Whittaker et al., 2001). Likewise, elucidating the trophic web dynamics that regulate nutrient and energy cycles requires knowledge of which species share a given space and time (Montoya et al., 2006). Characterising communities by studying their composition and structure, and understanding their spatio-temporal variation is

imperative to assess and monitor changes in ecosystems and biodiversity (Barnosky et al., 2012; Sala, 2000), and to develop conservation priorities and policies (Pereira et al., 2013).

Elevational gradients have increasingly been seen as a powerful model system to disentangle the relative effects of environmental factors on biodiversity because this allows for many replicates, enables experiments and facilitates data collection (Körner, 2007; Nogués-Bravo et al., 2008; Sanders and Rahbek, 2012). Gradients in temperature and humidity along elevations are usually matched by changes in species abundance and composition as well as in trait-based functional community structure (Fitzpatrick et al., 2013; Graham et al., 2014;

\* Corresponding author. Biodiversity Research Institute and Department of Evolutionary Biology, Ecology and Environmental Sciences, Universitat de Barcelona, Av. Diagonal 645, 08028 Barcelona, Spain.

E-mail address: [jagoba.malumbres.olarte@gmail.com](mailto:jagoba.malumbres.olarte@gmail.com) (J. Malumbres-Olarte).

<https://doi.org/10.1016/j.actao.2018.02.012>

Received 10 October 2017; Received in revised form 17 February 2018; Accepted 23 February 2018

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Sundqvist et al., 2013). With regard to species richness along elevational gradients, a number of diversity models have been put forward (Graham et al., 2014), those most commonly referred to being of two kinds: models that predict a monotonic decrease in the number of species with altitude, and models that expect a hump-shaped pattern with a peak in the middle of the gradient (Nogués-Bravo et al., 2008; Rahbek, 1997). Both model types can be based on the richness-productivity hypothesis (Grytnes, 2003; MacArthur, 1965; Rosenzweig, 1971; Wright, 1983). However, the former may also derive from hypothesised positive relationships between species richness and area or species distribution (Rapoport's rule) (Sanders, 2002; Stevens, 1992; Willig et al., 2003), whereas the latter include Mid-Domain-effect models (Colwell and Lees, 2000; Rahbek, 1997).

The Eastern Arc Mountains (EAM), Tanzania, provide an ideal system to study diversity patterns, with elevational gradients from 300 to 2400 m a.s.l. The EAM are classified as one of the world's biodiversity hotspots (Myers et al., 2000) and their forests are considered some of the oldest and most stable on the African continent (Loader et al., 2014), forming an 'inland archipelago'. The limited research that has been conducted in the EAM, mainly in the Udzungwa Mountains, Uluguru Mountains, and the East and West Usambara Mountains, has revealed elevated levels of biodiversity (Nyundo, 2002; Scharff, 1992; Sørensen, 2004; Sørensen et al., 2002) and in particular a remarkable endemism compared to the surrounding savanna and lowland forest. However, no comprehensive studies of the arthropod communities have been conducted yet.

Spiders are one of the most diverse groups of organisms both taxonomically and ecologically. Over 46,000 species and around 4000 genera have been described worldwide (World Spider Catalog, 2017) and many thousands more await discovery. The myriad of habitats and feeding adaptations of spiders, and their role as one of the dominant groups of arthropod predators in terrestrial ecosystems (Marc et al., 1999), make them indicators of changes in other arthropod communities and of habitat disturbance (Cardoso et al., 2010; Malumbres-Olarte et al., 2013; Moretti et al., 2002; Romero and Harwood, 2010; Wise, 1993).

Here we present the first characterisation of megadiverse spider communities along elevational gradients based on optimised and standardised sampling. Our aims are: 1) to test which elevational diversity model matches best the spider species richness in the Udzungwa Mountains; 2) to measure the variation in taxonomic structure among communities within and between elevations; and 3) to tease apart the contribution of each functional group (predatory guilds) and the spiders living in each microhabitat to the changes in communities along elevations.

## 2. Material and methods

### 2.1. Study area

Our study area is the Udzungwa Mountains (7.82°S, 36.70°E), Tanzania, which are recognised as a priority conservation area for mammals and birds (Dinesen et al., 2001) as well as for plants (Lovett et al., 1988; Lovett and Thomas, 1986). The Udzungwa Mountains are located in the southern part of the Eastern Arc Mountains and their forests are believed to have endured through millions of years due to long-term climatic stability (Lovett, 1993). Our plots lie on the eastern slopes of the Udzungwa Mountains National Park (UMNP; 12 plots) and in the Uzungwa Scarp Forest Reserve to the south (three plots) (Fig. 1, Table 1).

Due to the climatic influence of the Indian Ocean, the eastern slopes of the Udzungwa Mountains experience a high average annual rainfall of 2000 mm (Mumbi et al., 2008), with a heavy rainy season between March–May and a lighter rainy season between November–February (Lovett, 1996). There is a gradient in forest type from deciduous miombo (*Brachystegia* spp.) woodland in the lowlands (300 m a.s.l.) to

evergreen montane rainforest just below the highest peaks (2400 m a.s.l.), which are covered by a mosaic of bamboo (*Sinarundinaria alpina* (K. Schum.) C.S. Chao & Renvoize) and *Hagenia abyssinica* (Bruce) J.F. Gmel. woodlands (Lovett et al., 2006; Rovero et al., 2017). The frequent mist in the highest parts of the mountains results in high levels of precipitation through condensation and more humid conditions during the dry season (June–October).

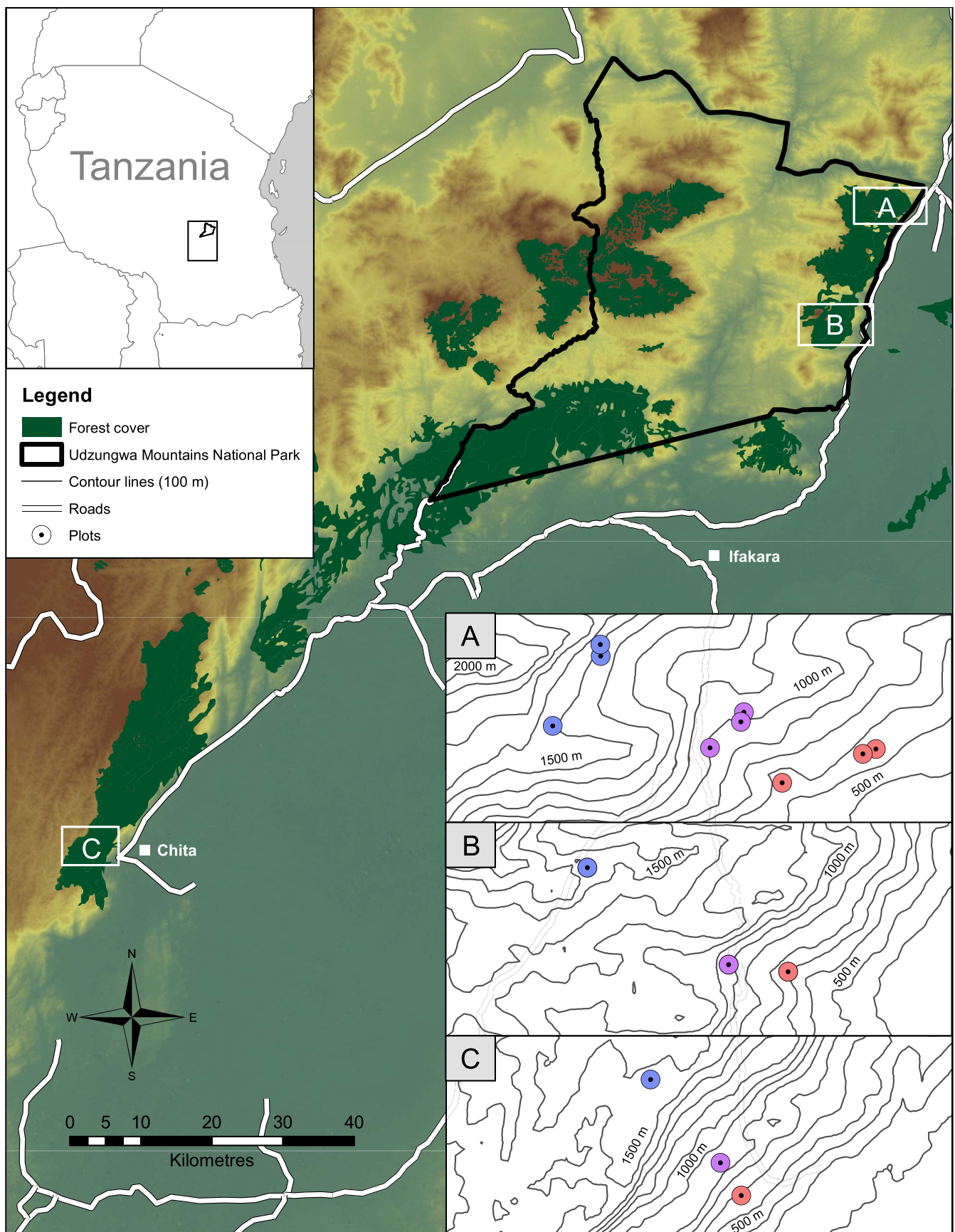
### 2.2. Sampling

We set up five elevational transects, each with a plot at each of the three target elevations (300–800, 800–1400 and 1200–1500 m a.s.l.) (Table 1), which correspond to three different forest types (lowland forest, submontane forest and montane forest, respectively) (Lovett, 1999, 1993). The five transects were separated horizontally by different distances – between the first and the remaining transects there were 0.1, 1, 20 and 175 km. Each plot was a 50 m × 50 m square (0.25 ha), within which we applied the COBRA-TF sampling protocol for spiders (Malumbres-Olarte et al., 2017) in October–November 2014. The COBRA protocol (Conservation Oriented Biodiversity Rapid Assessment) combine samples using different sampling methods to obtain the largest possible number of species for a given amount of effort (hence optimised) (Cardoso, 2009). More specifically, the COBRA-TF protocol (for tropical forest spiders) includes samples from different microhabitats (defined here as vegetation strata) of a tropical forest (see Malumbres-Olarte et al., 2017 for a full description) and may provide a reliable sample of the diversity and structure of the community at a given location (Cardoso, 2009). As required by COBRA-TF, in each plot we collected 36 samples: 8 samples of nocturnal aerial hand collecting, 6 samples of diurnal vegetation beating, 2 samples of nocturnal vegetation beating, 2 samples of diurnal ground hand collecting, 2 samples of nocturnal ground hand collecting, 2 samples of diurnal sweep netting, 2 samples of nocturnal sweep netting and 12 pitfall samples (where each sample consisted of four pitfall traps running for two weeks) (Malumbres-Olarte et al., 2017). These methods and samples can be classified according to the microhabitat (or stratum/height of vegetation) that they are applied to: ground (ground hand collecting and pitfall trapping), herbaceous vegetation (sweep netting) or low canopy (aerial hand collecting and vegetation beating). Each sample (except for the pitfall samples) consisted of an hour of collecting by a collector moving within the plot so that they covered as much area of the plot as possible. The 36 samples collected in each plot provided the data to calculate the diversity, given the number of samples, and obtain the composition of the corresponding spider community (Cardoso, 2009).

### 2.3. Data analyses

We assessed the thoroughness of our sampling by evaluating rarefied species accumulation curves visually and calculating the sampling completeness using the Chao 1 species estimator (Magurran and McGill, 2011; Scharff et al., 2003). We analysed the species diversity in the spider communities by calculating observed and estimated numbers of species (Jackknife 1 and 2, Chao 1 and 2 and ACE estimators), the percentage of adults, and the number of individuals and species of each predatory guild (defined as a group of spiders that share resources (Cardoso et al., 2011) for each plot and elevation). To test for differences in communities between elevations we ran a series of models and applied Tukey tests: generalised linear models for percentages of adults, and of individuals and species of different guilds and microhabitats; and ANOVAs for accumulated number of species, observed and estimated numbers of species, and number of rare species (species represented by one or two specimens).

To examine the similarity in species composition and relative abundance between spider communities we generated presence/absence (Sørensen index) and relative abundance (Steinhaus index)



**Fig. 1.** Study area and plots. Close-ups show the plots in the Udzungwa Mountains National Park (A and B) and in the Uzungwa Scarp Forest Reserve (C). Plots are coloured according to whether they were at low (red), mid (purple) and high (blue) elevations. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)



**Table 1**

Location (geographic coordinates in decimal degrees and altitude) and climatic features, sampling efficiency and observed number of species of sampling plots.

Plot	Latitude	Longitude	Altitude (m.a.s.l.)	Elevation	Sampling completeness (S/S*)	Observed species richness (S)	Estimated species richness (Chao 1) (S*)
1	−7.687091	36.94129	650.212	Low	71%	115	162.6
2	−7.687496	36.94022	649.972	Low	68%	136	201.0
3	−7.684011	36.93038	1004.936	Mid	63%	119	189.3
4	−7.684797	36.93014	993.160	Mid	68%	135	199.8
5	−7.679317	36.91859	1447.860	High	72%	134	185.8
6	−7.678377	36.91857	1481.747	High	72%	124	171.6
7	−7.689854	36.93354	707.651	Low	74%	143	193.5
8	−7.686934	36.92758	977.779	Mid	59%	126	214.5
9	−7.685076	36.91458	1526.688	High	72%	135	188.5
10	−7.841573	36.86703	674.245	Low	66%	125	188.1
11	−7.840599	36.85917	1006.378	Mid	68%	110	162.2
12	−7.827731	36.84056	1551.922	High	79%	126	159.4
13	−8.503722	35.91915	659.345	Low	75%	108	143.2
14	−8.499499	35.91654	908.324	Mid	80%	116	144.7
15	−8.488775	35.90760	1531.494	High	83%	127	152.2

dissimilarity matrices (Legendre and Legendre, 1998) and created an ordination through non-metric multidimensional scaling (NMDS) (McCune and Grace, 2002). We tested for differences between the 15 communities using ANOSIM (Bray-Curtis index, 999 permutations). We assessed the changes in beta diversity between elevations by calculating rarefied Jaccard and Sørensen pair-wise measures at each elevation and estimating their confidence intervals, as implemented in the R package BAT (Cardoso et al., 2015). Finally, we compared the species abundance distribution (SAD) curves of the communities and the alpha parameter values of the Gambin model (Matthews et al., 2014; Ugland et al., 2007). We based the Gambin model on species abundances rarefied (1000 permutations) by the minimum number of adult individuals per plot. Before these three analyses, we applied the Hellinger transformation to equalise species weights (Legendre and Gallagher, 2001). We handled and analysed all the data in R3.2.3 (R Development Core Team, 2017) using various packages including *vegan* (Oksanen et al., 2017) and *BAT* (Cardoso et al., 2015).

### 3. Results

The sampling yielded 40,613 individuals, of which 17,191 (42.3%) were adults. We observed 631 species or morphospecies belonging to 52 families and estimated between 784 and 866 species across all the plots (Fig. 2a). The number of species per plot (alpha diversity) varied between 108 and 143, and the total number of species at each elevation (5 plots) was similar as well as the beta diversity among the communities at each elevation (Jaccard and Sørensen indices) (Table 2). We obtained a sampling completeness of 79% for all communities and values between 59 and 83% for individual communities (Table 1). The species accumulation curves of the communities in the low plots had significantly steeper curves than the communities in mid and top plots (ANOVA,  $F_{2,12} = 8.81$ ,  $p < 0.01$ ;  $p_{\text{mid} < \text{low}} < 0.05$ ,  $p_{\text{high} < \text{low}} < 0.01$ ) (Fig. 2b and c).

Samples contained significantly higher percentages of adults at higher elevations (binomial [logit] distribution model,  $z_{\text{high} > \text{mid}} = 12.65$ ,  $p < 0.001$ ;  $z_{\text{high} > \text{low}} = 18.96$ ,  $p < 0.001$ ;  $z_{\text{mid} > \text{low}} = 6.93$ ,  $p < 0.001$ ) (Fig. 3b) but the number of spiders (individuals), and the observed (Fig. 3c) and estimated (Fig. 3d) numbers of species were not significantly different across all three elevations (Fig. 3a). The number of rare species decreased with elevation (Fig. 3e), although not significantly.

The NMDS on species presence and absences and relative abundance showed similar results, with a clear separation of the communities according to their elevation (Fig. 4 shows NMDS on Steinhaus index). The ANOSIM confirmed significant differences between plots at the three elevations (Fig. 5). The shape of the SAD curves and the values of the alpha parameter provided by the Gambin model showed that the

relative abundances of species in the low and mid elevation communities were similar (Fig. 6a and b). Some of the high elevation communities had slightly more even SAD curves and higher alpha values.

As for the microhabitat allocation, there were proportionally fewer ground spiders in the top plots (binomial [logit] distribution model,  $z_{\text{high} < \text{mid}} = 19.70$ ,  $p < 0.001$ ;  $z_{\text{high} < \text{low}} = 14.50$ ,  $p < 0.001$ ) and more low canopy individuals at high elevations ( $z_{\text{high} > \text{mid}} = 12.52$ ,  $p < 0.001$ ;  $z_{\text{high} > \text{low}} = 17.82$ ,  $p < 0.001$ ) (Fig. 7a). The number of species per microhabitat remained similar across elevations (Fig. 7b). The percentages of species belonging to the eight guilds defined by Cardoso et al. (2011) were similar (Fig. 8a) with one exception: there were significantly more species of sheet web weavers at high elevation ( $z_{\text{high} > \text{low}} = 3.40$ ,  $p < 0.01$ ;  $z_{\text{high} > \text{mid}} = 2.86$ ,  $p < 0.05$ ). The percentages of individuals of different guilds varied between elevations (Fig. 8b). With respect to the number of spiders, in the high elevation plots there were proportionally more ambushers ( $z_{\text{high} > \text{mid}} = 8.42$ ,  $p < 0.001$ ), sheet web weavers ( $z_{\text{high} > \text{mid}} = 10.36$ ,  $p < 0.001$ ) and other hunters ( $z_{\text{high} > \text{mid}} = 9.59$ ,  $p < 0.001$ ) than in the mid elevation plots. In the low elevation plots sensing web weavers ( $z_{\text{mid} < \text{low}} = 3.35$ ,  $p < 0.01$ ;  $z_{\text{high} < \text{low}} = 4.33$ ,  $p < 0.001$ ) and space web weavers ( $z_{\text{mid} < \text{low}} = 10.13$ ,  $p < 0.001$ ;  $z_{\text{high} < \text{low}} = 10.76$ ,  $p < 0.001$ ) were more abundant. Specialists were the most abundant at mid elevations and the least at low elevation ( $z_{\text{mid} > \text{low}} = 21.88$ ,  $p < 0.001$ ;  $z_{\text{high} > \text{low}} = 6.63$ ,  $p < 0.001$ ;  $z_{\text{high} < \text{mid}} = 21.56$ ,  $p < 0.001$ ). There were more orb web weavers in the top plots ( $z_{\text{high} > \text{low}} = 4.63$ ,  $p < 0.001$ ;  $z_{\text{high} > \text{mid}} = 3.53$ ,  $p < 0.01$ ).

### 4. Discussion

This study is the largest study of spider communities so far, in terms of observed species richness, habitat and microhabitat coverage and number of communities. Our species richness values surpass those of previous studies in other tropical areas (Baldissera et al., 2012; Coddington et al., 2009; Floren and Deeleman-Reinhold, 2005; Pinkus-Rendon et al., 2006; Pinto-Leite and Rocha, 2012), with the only exception of the survey conducted in Peru, where 1140 morphospecies were observed (Silva-Davila and Coddington, 1996). There are likely to be other spider communities that are even more species-rich, perhaps in the forests of the neotropics, and the sampling design and methodology used in this study can certainly help discover, survey and analyse them. The relatively high sampling completeness for all plots at all three elevations testify to the thoroughness of our sampling, and therefore the adequate characterisation of the spider communities (Table 2).

#### 4.1. Elevational diversity model

Contrary to our expectations of elevational changes in diversity, the

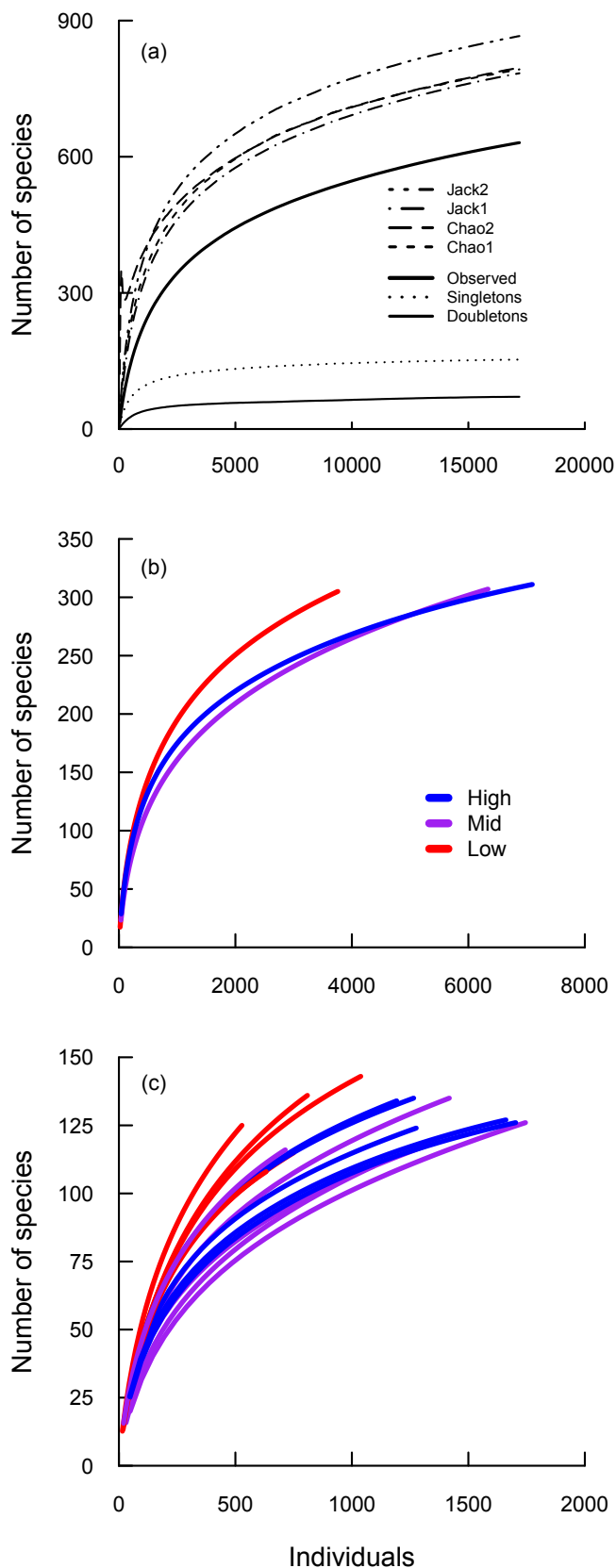


Fig. 2. Number of species in the study plots over the number of collected spider individuals. a) Observed and estimated number of species in all plots. b) Rarefied accumulated number of species at each elevation. c) Rarefied accumulated number of species in each plot.

observed and estimated numbers of species in each plot were very similar at the three elevations, and therefore the diversity patterns did not match any of the elevational models of species diversity. Indeed, communities have been found to track gradients along elevations (Graham et al., 2009; Machac et al., 2011; Peters et al., 2016), and several possible explanations have been put forward for changes in the number of species, including range size (Stevens, 1992), productivity (Hutchinson, 1959), environmental filtering (Graham et al., 2009; Maglianesi et al., 2015), geographic constraints (Colwell and Lees, 2000) and competition (Graham et al., 2009). More specifically, in the Udzungwa Mountains the number of species of plants, rodents and mollusks have been found to increase with elevation in a manner that fits with the mid-domain effect (Lovett et al., 2006; Stanley and Hutterer, 2007; Tattersfield et al., 2006). However, the differences among the spider communities resided in their species composition (Figs. 4 and 5) and, to a certain point, relative species abundances (Fig. 6a and b).

The simplest explanation for the similarity in the number of species may be that the differences in climatic and habitat conditions along the modest elevation range (700–1500 m) are too small to result in significant differences in the number of spider species collected with the applied sampling protocol. Climatic homogeneity can almost certainly be ruled out since we found differences of up to 5 °C and 10% of humidity between the low and high elevation plots. As for the habitat conditions, there have been suggestions that the forests of the Udzungwa Mountains are homogeneous between 300 and 1850 m (Lovett et al., 2006), despite the finding that the species composition of birds and amphibians change elevationally (Poynton et al., 2007; Romdal and Rahbek, 2009).

We therefore propose another possible explanation based on niche availability (Greenstone, 1984; Malumbres-Olarte et al., 2013; Riechert and Gillespie, 1986) and environmental filtering (Chatzaki et al., 2005; Foord and Dippenaar-Schoeman, 2016). If the number and structure of available niches for spiders are also similar at different elevations, the number of species and the functional types that each elevation can contain may be similar. However, due to differences in climatic adaptations between species (environmental filtering), distinct spider communities may be found at different elevations. Considering the importance of the physical structure of (micro)habitats for spiders, testing our hypotheses may require studies that incorporate detailed data on space, physical three-dimensional structure and (micro)climatic conditions.

We found that the percentage of adult spiders was greater at higher elevations, which may be the result of sampling at the end of the dry season, when forests at low elevations are considerably drier. Adults are individuals that have reached the reproductive stage and may require more prey (especially females) for themselves and their growing gonads. Therefore, the percentage of adults of most species may be higher when climatic conditions are most favourable and more prey is available (Cardoso et al., 2007; Gasnier et al., 2002). This ‘favourable time-window’ is often when the most limiting resource is most abundant. For instance, late spring-early summer may be the time with the highest percentages of adults in Mediterranean ecosystems (Cardoso et al., 2007) because combination of temperature and rain/humidity conditions is optimal for producing offspring, whereas it may be in late summer in subalpine areas where water is never scarce and when the average daily temperature is the highest (Malumbres-Olarte, 2011). However, in the absence of strong seasonal changes there may not be any ‘favourable time-windows’, and the percentage of adults may be stable throughout the year. This may be the case for the higher elevation plots, where levels of humidity are higher (pers. obs. with data loggers) and may be less influenced by dry and wet seasonal cycles. To test whether this hypothesis is true, future observational studies should look for associations or correlations between seasonal variability in climatic conditions, breeding seasonality and variability in percentage of adults. It is also possible that the greater number of adults may be the

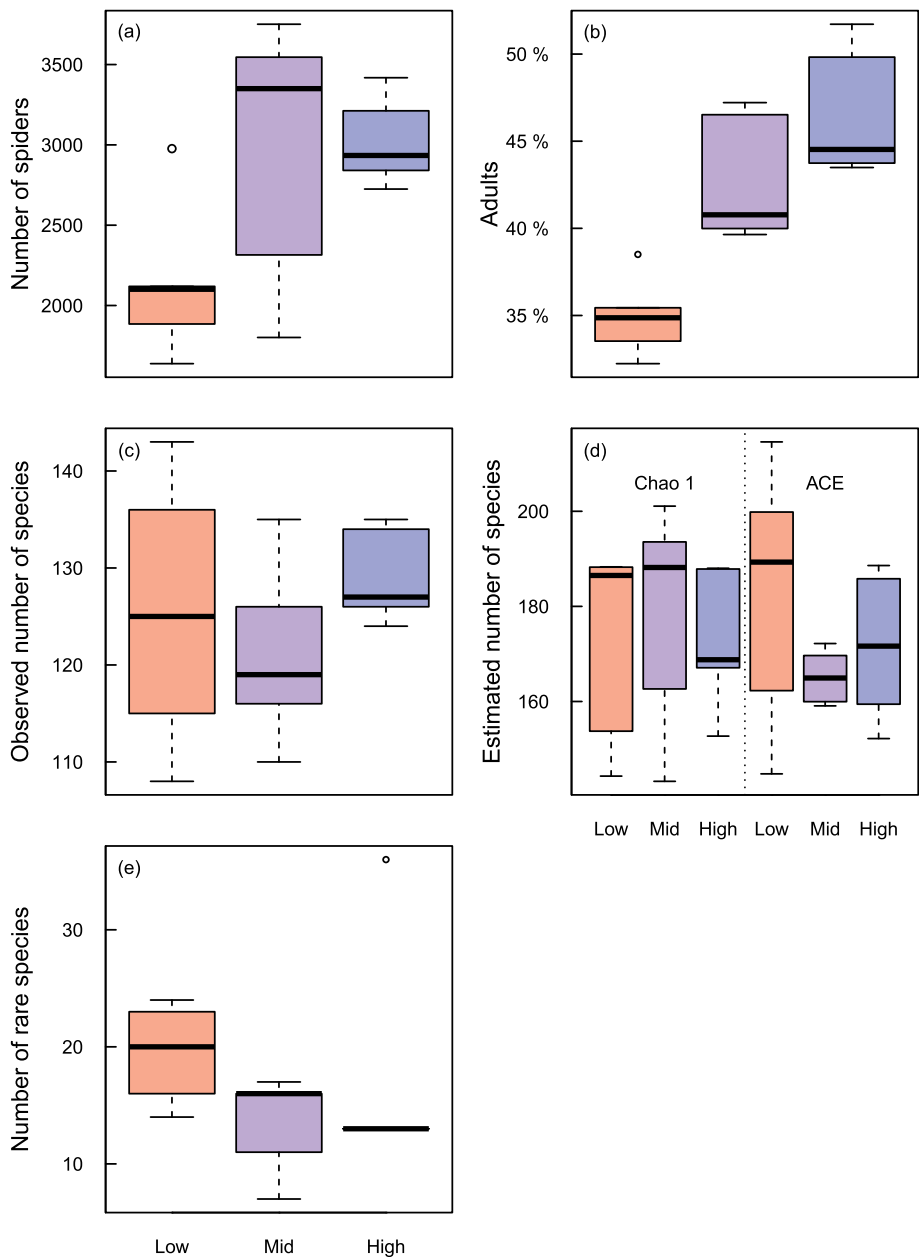
**Table 2**  
Total observed and estimated number of species (Chao 1), sampling completeness and beta diversity for each of the three elevations. Beta diversity measures were calculated from rarefied communities at the same elevation – mean values and confidence intervals.

Elevation	Observed species richness	Estimated species richness ( ± s.e.m.)	Sampling completeness	Beta Jaccard (95% CI)	Beta Sørensen (95% CI)
Low (~700 m.a.s.l.)	305	398.52 ± 11.80	77%	0.70 (0.68, 0.71)	0.54 (0.53, 0.56)
Mid (~1000 m.a.s.l.)	307	418.05 ± 10.23	73%	0.74 (0.72, 0.75)	0.59 (0.57, 0.62)
High (~1500 m.a.s.l.)	311	386.77 ± 13.92	80%	0.71 (0.69, 0.73)	0.57 (0.55, 0.59)

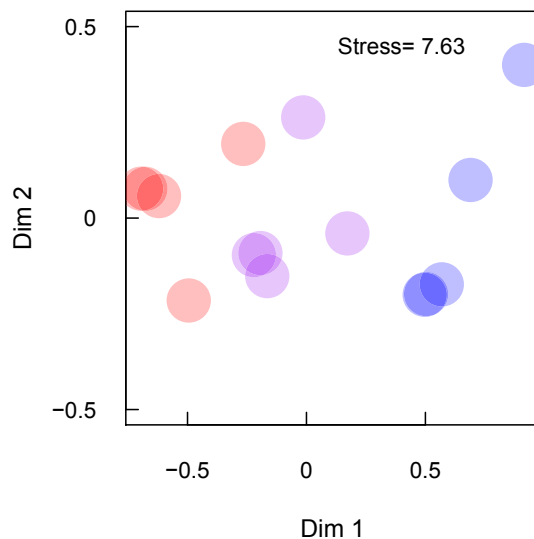
result of more intense and efficient sampling at high elevations, which would also explain the lower number of rare species collected there (Coddington et al., 2009).

4.2. Variation in taxonomic, functional and microhabitat community structures

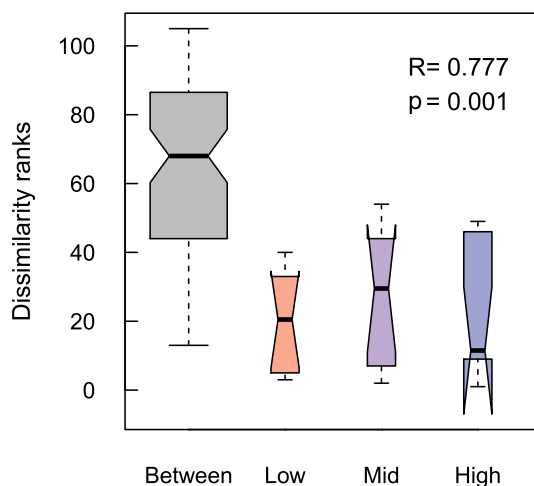
Although the alpha and beta diversity, and the species richness at each elevation remain the same at all three elevations, the species composition does change. The latter could be accredited to the changes in microhabitat composition, availability and structure, and the



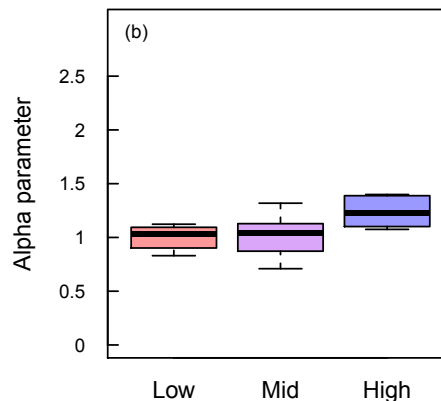
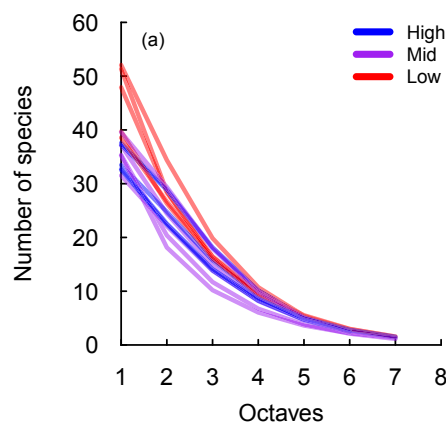
**Fig. 3.** Diversity values for the sampling plots in low (red), mid (purple) and high (blue) elevations. a) Number of spider individuals per plot. b) Percentage of adults per plot. c) Observed number of species per plot. d) Estimated number of species (Chao 1 and Abundance Coverage Estimator) per plot. e) Number of rare species (species represented by one or two specimens in the entire dataset) at each elevation. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)



**Fig. 4.** Abundance-based species similarity among the studied communities, illustrated by non-metric multidimensional scaling of Bray-Curtis similarity index. Colours represent plots at low (red), mid (purple) and high (blue) elevations. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)



**Fig. 5.** Dissimilarity values among the spider communities obtained from an ANOSIM based on Bray-Curtis dissimilarity index.



**Fig. 6.** Species abundance distributions using the Gambin model. Curves (a) and alpha values (b) for each of the 15 spider communities at the three elevations.

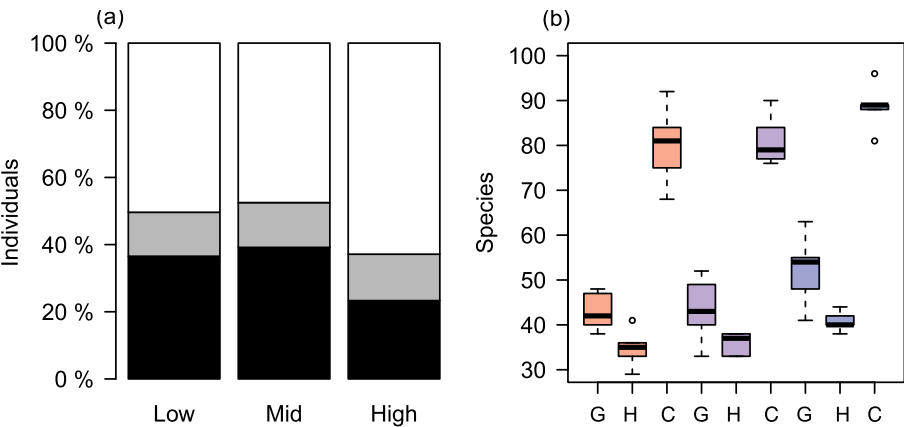
associated adaptations of the species. The fact that there were fewer spiders on the ground and more in the canopy at high elevations (Fig. 7a) may be explained by either greater space available to spiders or greater density of spiders in the canopy microhabitat. If density fluctuates and, as we found, the number of species per microhabitat remains similar across elevations, it may be possible that interspecific competition also varies. If so, our results may suggest that interspecific competition for low canopy microhabitat is greater at low elevations than at higher elevations.

Differences in microhabitat community structure are also reflected by the relative abundances of the spiders belonging to different predatory guilds. High elevation communities have more ambushers, orb web weavers and other hunters, many of which are shrub and tree dwellers and are present in the low canopy (Fig. 8b). Likewise, sensing web and space web weavers include ground spiders and abound more at low elevation.

Indeed, the megadiverse spider communities of the Udzungwa Mountains change taxonomically and functionally across habitats and microhabitats. Our findings suggest that the regional and local-scale processes behind these patterns may depend on the characteristics of the habitats (temperature, humidity, forest physical structure) and the microhabitat structure (total and relative space covered by each microhabitat, physical three-dimensional structure), and we encourage future studies to incorporate detailed data on them.

#### 4.3. Repercussions for conservation

Our findings support the notion that safeguarding the biotic communities of the Udzungwa Mountains, and probably of other parts of the Eastern Arc Mountains, requires protecting areas with different ecosystems and habitats. This is of utmost importance in the Udzungwa Mountains given the current pace of vegetation degradation and habitat loss and fragmentation (Barelli et al., 2015) in unprotected or semi-protected areas outside the National Park, such as the Kilombero Nature Reserve and Uzungwa Scarp Forest Reserve (Hegerl et al., 2017; Rovero et al., 2015). Unlike the areas within the National Park, the natural vegetation of the surrounding lands have become severely degraded in recent decades (Brink et al., 2016), so legal protection may be necessary to conserve native vegetation, and thereby native arthropod communities associated with it. The negative effects of human disturbance on mammals have been used to point out the urgent need for better protection of the EAM forests (Rovero et al., 2017). Here we make the point that the spatial distribution of biodiversity of less iconic but more diverse taxa should also be taken into consideration, so that protected areas includes a variety of climatic conditions and habitat types that allow their continued survival.



**Fig. 7.** Diversity values in each stratum of the vegetation at the three elevations. a) Percentage of spider individuals on the ground (black), in herbaceous vegetation (grey) and in the low canopy (white). b) Number of species in ground (G), herbaceous (H) and low canopy (C) vegetations in low (red), mid (purple) and high (blue) elevation plots. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

**Contribution of the authors**

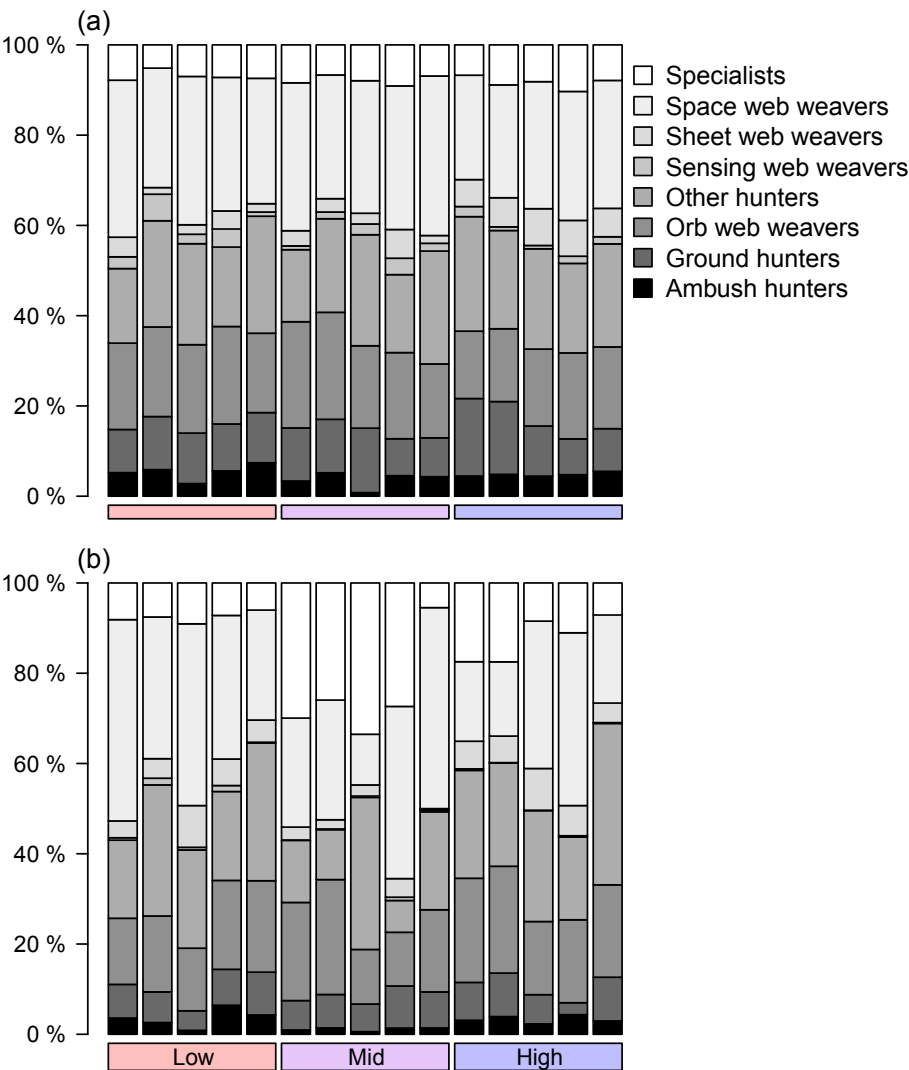
JMO, NS, TP and PC conceived and designed the study and the sampling. JMO, LC, PC and TS collected the samples, JMO, LC and WF generated the data from the samples, and JMO analysed the data. NS and TP provided the logistical and financial support from grants (see acknowledgements). JMO, NS, PC and TP wrote the paper and all authors approved it.

**Compliance with ethical standards**

This study does not infringe any bio-ethical principles.

**Conflicts of interest**

The authors had no conflict of interest.



**Fig. 8.** Percentages of spiders of different predatory guilds in the 15 communities. a) Percentage of species per plot. b) Percentage of individuals per plot.



## Acknowledgements

NS and JMO acknowledge the Danish National Research Foundation for the funding (grant no. 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). 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 do research in the Udzungwa Mountains National Park. Richard M. L. Laizze and Aloyce Mwakisoma provided invaluable assistance in the field, and the Udzungwa Ecological Monitoring Center (UEMC) and its staff provided logistical support. We also thank Bjørn Hermansen, Natural History Museum of Denmark, for his help with GIS data.

## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.actao.2018.02.012>.

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