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

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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 reflex 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;

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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 endemicity 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)